



A review of Norwegian streptaster-bearing Astrophorida (Porifera: *Demospongiae: Tetractinellida*), new records and a new species

PACO CÁRDENAS^{1,2,*} & HANS TORE RAPP^{1,3,4}

¹ Department of Biology, University of Bergen, PO Box 7803, N-5020 Bergen, Norway. E-mails: cardenas_paco@yahoo.fr; hans.rapp@bio.uib.no

² Muséum National d'Histoire Naturelle, Département Milieux et Peuplements Aquatiques, UMR "BOREA" 7208, 43 rue Cuvier, 75005, Paris, France

³ Centre for Geobiology, University of Bergen, Allégaten 41, 5007 Bergen, Norway

⁴ Uni Environment, Thormøhlensgate 49B, N-5006 Bergen, Norway

* Current address: Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, S-75236 Uppsala, Sweden.

Abstract

We report and describe new material of streptaster-bearing Astrophorida sponges collected in Norway: *Characella pachastrelloides*, *Pachastrella nodulosa* **sp. nov.**, *Poecillastra compressa*, *Vulcanella* cf. *aberrans*, *Thenaea abyssorum*, *Thenaea levis*, *Thenaea muricata* and *Thenaea valdiviae*. Because many of these species were described in the end of the 19th century their original descriptions are often incomplete. The Norwegian specimens are the basis for a revision of the morphology, taxonomy and distribution of these species. These are the first records of *C. pachastrelloides* and *V.* cf. *aberrans* from the Norwegian coast. *Pachastrella nodulosa* **sp. nov.** differs from *Pachastrella monilifera* by (i) its knobby surface and (ii) the absence of large oxeas, (iii) its amphiasters have on average less actines and are less spiny, finally (iv) microxeas are rare and with a distinct morphology (although there is some doubt concerning their origin). In the present study, *Characella tuberosa* (from South Africa), *Pachastrella abyssi* (from the North-West Atlantic) and *Thenaea schmidtii* (from the North-East Atlantic) are resurrected. To help their future identifications, all the Norwegian species described were associated with DNA barcodes: a cytochrome *c* oxidase subunit I (COI) gene partial fragment and/or a 28S ribosomal gene partial fragment (C1–D2 domains). Furthermore, a key to the streptaster-bearing Astrophorida of the North-East Atlantic and the Mediterranean Sea is also given (lithistids not included).

Abstract [French]

Nous signalons la présence et décrivons des spécimens d'Astrophorida à streptasters nouvellement récoltés en Norvège: *Characella pachastrelloides*, *Pachastrella nodulosa* **sp. nov.**, *Poecillastra compressa*, *Vulcanella* cf. *aberrans*, *Thenaea abyssorum*, *Thenaea levis*, *Thenaea muricata* et *Thenaea valdiviae*. Plusieurs de ces espèces ont été décrites de manière incomplète à la fin du 19^{ème} siècle. Les spécimens norvégiens sont l'occasion de réviser la morphologie, la taxonomie et la distribution de ces espèces. C'est la première fois que *C. pachastrelloides* et *V.* cf. *aberrans* sont mentionnés sur la côte norvégienne. *Pachastrella nodulosa* **sp. nov.** se distingue de *Pachastrella monilifera* par (i) sa surface noduleuse et (ii) l'absence de grands oxes, (iii) ses amphiasters ont en moyenne moins d'actines et sont moins épineux, enfin (iv) les microxes sont rares et ont une morphologie distincte (bien qu'il y ait encore des doutes sur leur origine). Au cours de notre étude, *Characella tuberosa* (d'Afrique du Sud), *Pachastrella abyssi* (de l'Atlantique Nord-Ouest) et *Thenaea schmidtii* (de l'Atlantique Nord-Est) sont ressuscités. Afin d'aider leurs identifications futures, toutes les espèces de Norvège décrites ont été associées à des code-barres moléculaires: un fragment partiel du gène de la sous-unité I du cytochrome *c* oxydase (COI) et/ou un fragment partiel du gène ribosomique 28S (domaines C1-D2). De plus, une clé pour identifier les Astrophorida à streptasters de l'Atlantique Nord-Est et de Méditerranée est également fournie (lithistides non inclus).

Key words: Taxonomy, *Characella*, *Poecillastra*, *Pachastrella*, *Vulcanella*, *Thenaea*, Pachastrellidae, DNA barcodes, Norway, cosmopolitanism.

Introduction

The Norwegian coast extends from 57°57'N to 71°11'N, or through more than 13° of latitude (Brattegard & Holthe 1997). This very long coastline includes a wide range of habitats, ranging from small and sheltered brackish lagoons to fjords of more than 1300 m depth, and to a highly exposed and topographically diverse outer coastline and a wide continental shelf. The coast is characterized by two different water masses, the Atlantic warm and high-saline water (>35 S) and the coastal water with lower salinity (<35 S) and more variable temperatures (Breen 1990). Throughout the Norwegian coast and shelf there are distinct gradients in temperature, salinity, tidal amplitude and bottom type, resulting in a rich and varied marine fauna. Around 300 sponge species from the Norwegian coast have so far been reported (Tendal *et al.* 2001; Oug & Rapp 2010). Although sporadically studied, the sponge fauna represents one of the most diverse macrobenthic animal groups in the Norwegian fjords and coastal areas. More recent investigations have resulted in many new species for science (Rapp *et al.* 2001; Rapp 2006), a number of new records for this region (Cárdenas *et al.* 2007; Tornes 2008; Thomassen 2009) and an increasing number of more southern species reaching the Norwegian coast, possibly due to the effect of climate warming in the North-East Atlantic (NEA) (Narayanaswamy *et al.* 2010).

The Pachastrellidae *sensu* Maldonado (2002) is a worldwide Astrophorida family defined as having tetractinal megascleres in combination with streptaster microscleres (never euasters), and for most of them, monaxonic microscleres (e.g. microxeas). However, molecular evidence has clearly shown that streptasters in the Pachastrellidae *sensu* Maldonado (2002) is a plesiomorphic character (Cárdenas *et al.* 2011). Therefore, this family is polyphyletic and the genera have been i) considered as *incertae sedis* (*Characella* Sollas, 1886, *Acanthotriaena* Vacelet *et al.*, 1976, *Ancorella* von Lendenfeld, 1907), ii) reallocated to the Ancorinidae (*Dercitus* Gray, 1867 and *Stoeba* Sollas, 1888) or iii) distributed in three monophyletic families: Theneidae Carter, 1883, Pachastrellidae Carter, 1875 (with a new definition) and Vulcanellidae Cárdenas *et al.*, 2011 (Cárdenas *et al.* 2011). This major reorganization of the Pachastrellidae *sensu* Maldonado (2002) proposed by Cárdenas *et al.* (2011) is fairly recent. This review is therefore also an opportunity to present, explain and support the new classification of this group using morphological evidence on concrete examples. This explains why we review in this paper species from a polyphyletic group.

Streptasters *sensu* Sollas (1888) are asters in which the rays proceed from an axis that can be straight or spiral, so they are not true asters (euasters: e.g. oxyasters, strongylasters, sterrasters). Depending on their size, number of actines and shaft morphology, streptasters are categorized as spirasters (small, many actines, twisted long shaft), metastasters (intermediate morphology) and plesiasters (large, few actines, short or disappearing shaft). In some cases, when actines radiate from both ends of a straight shaft, the streptasters are called amphiasters. “Streptasters” found in some Ancorinidae genera (*Stryphnus* Sollas, 1886, *Ancorina* Schmidt, 1862, *Dercitus*, *Stoeba*) are morphologically different and should be called sanidasters (Sollas 1888, p. cxii): an aster with a straight rhabdal axis on which small actines branch. Most of streptaster-bearing Astrophorida are confined to deep-waters. They represent 122-128 valid described species worldwide (without lithistids) (van Soest *et al.* 2010). Of these, 26 are present in the NEA/Mediterranean region, of which five are currently recorded from Norway (Steenstrup & Tendal 1982; Tendal *et al.* 2001): *Pachastrella monilifera* Schmidt, 1868, *Poecillastra compressa* Bowerbank, 1866, *Thenia levis* von Lendenfeld, 1907, *Thenia muricata* (Bowerbank, 1858), and *Thenia valdiviae* von Lendenfeld, 1907. Many NEA species that were described early in the history of sponge taxonomy have been considered to be cosmopolitan and fairly common (e.g. *P. compressa*, *P. monilifera*, *T. muricata*, *Characella pachastrelloides* (Carter, 1876)). They seem to have surprisingly conserved morphologies over wide geographical areas. But at a time when most widespread sponge species are found to be cryptic species complexes (e.g. Cárdenas *et al.* 2007; Reveillaud *et al.* 2010; Xavier *et al.* 2010 and references therein), new specimens collected along the Norwegian coast were an opportunity i) to review the validity of these “common” species through a thorough reassessment of their morphology and ii) to add DNA barcodes to supplement the traditional species description.

Material and Methods

Specimens from western Norway were collected at four different localities in the Bergen area: Hjeltefjord (60°25'N, 05°06'E), Korsfjord (60°10'N, 05°10'E), Marstein (60°08'18"N, 4°50'47"E) and Langenuen (59°53'N, 05°31'E), using a triangular dredge (Hjeltefjord, Korsfjord, Langenuen) or a bottom trawl (Marstein) at depths between 80 and

600 meters. Other specimens were collected in northern Norway during the Polarstern ARK-XXII/1a cruise in June 2007, using the manned-submersible JAGO and boxcores: in Sotbakken (70°45'N, 18°40'E), Røst reef (67°30'N, 9°24'E) and Trænadjupet (66°58'N, 11°7'E). Finally, additional *Thenia* specimens were collected during the 'Ecosystem Barents Sea 2007' cruise (Institute of Marine Research) in the western Barents Sea and during the 'Møre 2006' cruise in western Norway. More specimens from the Norwegian coast were found in Museum collections. Distribution maps were made with Planiglobe (<http://www.planiglobe.com>) by adding the records of this study to existing localities taken from the literature. All freshly collected specimens were fixed in 96% ethanol soon after collection and stored at room temperature at the Bergen Museum and the University of Bergen.

To collect the spicules, sponge tissue was digested in chlorine. Spicules were then washed twice with water and once with ethanol 96%. A few drops of this solution was placed on a slide in a Eukitt™ mounting medium. 30 spicules per spicule type were measured, unless otherwise stated. Measurements of all spicules were made with a light microscope, except for the measurements of streptasters, made with the scanning electron microscope (SEM). Width of rhabdomes of triaenes was measured right under the cladomes. Width of the microxeas was measured in the middle. Some of these spicules were placed directly on top of a cover slip glass taped to a stub and coated with a gold/palladium mix. They were then observed with a ZEISS Supra 55V SEM at the University of Bergen. We followed Boury-Esnault *et al.* (2002) for preparation of thick sections (100–800 µm) with a diamond wafering blade and a low speed saw. Instead of epoxy resin, we used an Agar Low Viscosity Resin kit (© Agar Scientific) in accordance with the manufacturer's mixing instructions to make a hard embedding medium. *Thenia* sections were stained with a fuchsine-toluidine mix in order to reveal and measure choanocyte chambers. Sections were not polished but directly embedded in the resin between the cover slip and the slide. Digital pictures of these sections were taken with a Nikon camera fixed to a stereomicroscope (Leica M216 A).

Following the Sponge Barcoding Project (Erpenbeck *et al.* 2007; Wörheide *et al.* 2007), we sequenced the Folmer fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene and/or a 28S ribosomal gene partial fragment (C1–D2 domains) of our specimens (Table 1). These sequences were obtained and used in a previous phylogenetic study (Cárdenas *et al.* 2011). Sequences, along with the following descriptions of the Norwegian specimens, were submitted to the Sponge Barcoding Project: www.spongebarcoding.org.

TABLE 1. Locality of collection, museum voucher numbers and Genbank accession numbers of sequences available of streptaster-bearing North-East Atlantic Astrophorida examined in this study. Table modified from Cárdenas *et al.* (2011, Table S1). In bold, specimens collected on the Norwegian coast. Abbreviations: MNHN, Muséum National d'Histoire Naturelle, Paris; ZMA, Zoölogisch Museum van de Universiteit van Amsterdam; ZMBN, Bergen Museum.

Species	Voucher No.	COI	28S	Collection site
Astrophorida incertae sedis				
<i>Characella pachastrelloides</i>	ZMBN 80248	HM592672	HM592778	Hjeltefjord (western Norway)
<i>Characella pachastrelloides</i>	ZMAPOR 20375	HM592749	HM592781	Mingulay Reef, Scotland (United Kingdom)
<i>Characella pachastrelloides</i>	ZMBN 85225	HM592709	HM592780	Setúbal Canyon (Portugal)
<i>Characella pachastrelloides</i>	ZMAPOR 18041	HM592713	HM592779	Gulf of Cadiz (Spain)
Pachastrellidae				
<i>Pachastrella nodulosa</i> sp. nov.	ZMBN 85227 paratype	HM592698	HM592775	Korsfjord (western Norway)
<i>Pachastrella ovisternata</i>	ZMAPOR 21219	HM592748	-	Bay of Biscay (off France)
<i>Pachastrella ovisternata</i>	ZMAPOR 21224	-	HM592774	Gulf of Cadiz (Off Morocco)
Vulcanellidae				
<i>Poecillastra compressa</i>	ZMBN 77932	EU442192	-	Langenuen (western Norway)
<i>Poecillastra compressa</i>	ZMBN 85251	-	HM592757	Hjeltefjord (western Norway)
<i>Poecillastra compressa</i>	MNHN DCL4072	HM592714	AF062599	Banc de l'Esquive (France, Mediterranean Sea)
<i>Poecillastra compressa</i>	ZMBN 86300	HM592675	-	Rockall Bank (off Ireland)

..... continued on the next page

TABLE 1 (continued)

Species	Voucher No.	COI	28S	Collection site
<i>Vulcanella</i> cf. <i>aberrans</i>	ZMBN 80959	HM592699	HM592758	Sotbakken (northern Norway)
<i>Vulcanella aberrans</i>	ZMAPOR 21193	HM592700	-	Gulf of Cadiz (off Morocco)
<i>Vulcanella aberrans</i>	ZMAPOR 18012	-	HM592759	Gulf of Cadiz (off Morocco)
<i>Vulcanella gracilis</i>	ZMAPOR 18025	HM592702	-	off Tanger (Morocco)
<i>Vulcanella gracilis</i>	MNHN DCL4082	HM592704	HM592760	off Cape S. Maria di Leuca (southern Italy)
Theneidae				
<i>Thenea abyssorum</i>	ZMBN 85228	HM592712	HM592770	Greenland Sea
<i>Thenea levis</i>	ZMBN 85229	-	HM592764	Sotbakken (northern Norway)
<i>Thenea levis</i>	ZMBN 85230	HM592717	HM592765	Off Korsfjord (western Norway)
<i>Thenea levis</i>	ZMAPOR 21501	HM592747	HM592766	South West of Rockall Bank (off Ireland)
<i>Thenea muricata</i>	ZMBN 85231	-	HM592768	off Korsfjord (western Norway)
<i>Thenea muricata</i>	ZMBN 85232	HM592677	-	Brattholmen (western Norway)
<i>Thenea muricata</i>	-	-	AY552019 ^a	Perseverance Mound (off Ireland)
<i>Thenea muricata</i>	MNHN DCL4083	HM592706	HM592767	off Cape S. Maria di Leuca (southern Italy)
<i>Thenea schmidtii</i>	ZMAPOR 18036	HM592737	HM592769	Gulf of Cadiz
<i>Thenea valdiviae</i>	ZMBN 85233	HM592708	-	Barents Sea
<i>Thenea valdiviae</i>	ZMBN 85234	HM592694	HM592761	Greenland Sea
<i>Thenea valdiviae</i>	ZMBN 85235	HM592703	HM592762	Trænadjupet (northern Norway)
<i>Thenea valdiviae</i>	ZMBN 85236	HM592718	HM592763	off Korsfjord (western Norway)

^a C1-D1 domains (Borchiellini *et al.* 2004).

Abbreviations used in the text are as follows: BMNH (British Museum of Natural History, London); CEAB (Centro de Estudios Avanzados de Blanes); HBOI (Harbour Branch Oceanographic Institute, Fort Pierce, FL); MNHN (Muséum National d'Histoire Naturelle, Paris); MZS (Musée Zoologique de Strasbourg); NTNU-VM (Museum of Natural History and Archaeology, The Norwegian University of Science and Technology (NTNU), Trondheim); ZMA (Zoological Museum in Amsterdam); ZMBN (Bergen Museum).

RESULTS

Class DEMOSPONGIAE Sollas, 1885

Order ASTROPHORIDA Sollas, 1888

Genus *Characella* Sollas, 1886 *incertae sedis*

Diagnosis: Astrophorida with a majority of amphiasters as streptasters (never spirasters) and with at least two clearly separated categories of monaxonic spicules: the longest (microxea, microstyles, microstongyloxeas) and the smallest category (microrhabds with oxea or strongyle ends) (Cárdenas *et al.* 2011).

Note on phylogenetic position: Molecular data suggests that *Characella* is phylogenetically close to Astrophorida lithistids and belongs to a large clade temporarily called 'Clade A' which includes the Geodiidae, Ancorinidae, Pachastrellidae, Corallistidae, Theonellidae and Phymaraphiniidae (Cárdenas *et al.* 2011).

Characella pachastrelloides (Carter, 1876)

(Figures 1–3, Table 2)

Synonymy.

Stelletta pachastrelloides Carter, 1876: Carter 1876, p. 403.

Characella sollasi Topsent, 1890b: Topsent 1890b, p. 70; Topsent 1892, p. 40; Ferrer-Hernández 1914, p. 11.

Characella pachastrelloides: Sollas 1888, p. 407; Topsent 1904, p. 96; Stephens 1915, p. 14; Topsent 1928, p. 133; Arnesen 1932, p. 13; Lévi & Vacelet 1958, p. 231; Boury-Esnault *et al.* 1994, p. 46; Maldonado 1996, p. 394; Maldonado 2002, p. 148; van Soest *et al.* 2007, Table 2; Cárdenas *et al.* 2011, Table S1.

Stryphnus pachastrelloides (Schmidt, 1870): Burton 1954, p. 220.

Not *Ancorina pachastrelloides* Schmidt, 1870, p. 68 = *Characella connectens* Schmidt, 1870 according to Maldonado (2002).

Not *Poecillastra sollasi* (Topsent, 1892): van Soest & Stentoft 1988, p. 36 = *Poecillastra* sp. (this study).

Material. ZMBN 80248, Brattholmen, Hjeltefjord, western Norway, depth: 80–140 m, deep-water *Lophelia pertusa* reef, triangular dredge.

Comparative material examined.

Characella pachastrelloides, MNHN-DN22, Norman Collection, slide, Porcupine expedition; ZMAPOR 20375, Mingulay reef, Scotland, 56°49'27"N, 7°22'7"W, 128–137 m (Fig. 2C, E, G); ZMBN 25629, 35°32'N, 07°07'W, Ibero-Moroccan Gulf, 1215 m (Arnesen 1932) (Fig. 2B, H); ZMAPOR 18041, Gulf of Cadiz, Spain, 742 m; ZMBN 85225, 38°16'N, 9°10'W, Setúbal canyon, South Portugal, 1451 m (Fig. 2I); ZMBN 85241, Guilvinec Canyon, Bay of Biscay, 46°54'N, 05°19'W, 676–691 m. *Characella* cf. *pachastrelloides*, MNHN-DCL3228, Manila, Philippines, 170–200 m, MUSORSTOM 1, St. 51; MNHN-DCL3229, slide, Manila, Philippines, 198 m, MUSORSTOM 2, St. 1.

Characella tripodaria (Schmidt, 1868), MNHN-DT756, holotype, Algeria.

Characella tuberosa Lévi, 1964, MNHN-DCL1396, slide of holotype, 29°55'S, 31°20'E, Off Durban, South Africa, 430 m, Galathea expedition.

Poecillastra dilifera (de Laubenfels, 1934), MNHN-DNBE1, slide of paratype, Puerto Rico, 439–548 m.

Poecillastra sp., ZMAPOR 5300, originally identified as *Poecillastra sollasi* (van Soest & Stentoft 1988), off Paynes Bay, Barbados, 216 m, det. P. Cárdenas.

Outer morphology (Fig. 1A). ZMBN 80248 is a massive fragment 5 cm long and 4 cm wide. Surface and choanosome color in ethanol is cream. The specimen is not compressible. Surface is irregular, strongly hispid and dirty (due to trapped sediments). The specimen is partly stained purple due to the encrusting sponge *Hexadella dedriferifera* Topsent, 1913b which turns from bright yellow to purple in ethanol. There is no visible cortex. No oscules or pores were found.

Skeleton (Fig. 1D, F). There is no real separated cortex, just a dense accumulation of paratangential microxeas II, reinforced by an underlying dense layer of paratangential microxeas I. This layer is 150–200 µm thick, thus invisible to the naked eye. Both orthotriaenes and dichotriaenes are present, more or less positioned radially with their cladomes tangential to the cortex. Some oxeas and triaenes cross the surface; they are responsible of the strong hispidation. Apart from the radial position of some triaenes, the arrangement of the spicules in the choanosome is confused. Amphiasters are commonly found in the cortex area but are also moderately present in the choanosome. Both kinds of microxeas are abundant in the choanosome, but the microxeas I are clearly predominant and form a dense meshwork. There is also a contamination of *Geodia* sterrasters in the choanosome.

Spicules (ZMBN 80248) (Fig. 2). (a) oxeas I, stout, most are curved (once or twice), length: 2184–1769–1210 µm; width: 20–37–52 µm. (b) oxeas II, foreign?, slightly curved, smooth, sometimes modified to a style, rare, length: 300–381.4–438 µm (N=21); width: 9–11.7–13 µm (N=21). (c) ortho- and dichotriaenes, some with deformities such as irregular or additional clads, rhabdome length: 168–408–630 µm; rhabdome width: 11–33–49 µm; clad length for orthotriaenes: 83–175–316 µm (N=18); clad length for dichotriaenes: 70–99–129 µm + 72–135–194 µm (N=12). (d) amphiaster, 9–14 actines, microspiny, length: 13–18–29 µm. (e) microxea I, in high numbers, microspiny, usually straight but sometimes curved, sometimes modified to a microstyle, length: 80–195–259 µm; width: 2–4.4–5 µm. (f) microxea II, faintly microspiny, straight or bent, often centrotylotes, sometimes modified to a microstyle or a microstrongyle, length: 24–35–49 µm; width: 2–2.6–4 µm.

Distribution. (Fig. 3). Norway (this study); Scotland (this study); Porcupine Bank (van Soest *et al.* 2007); Ireland (Stephens 1915); Portugal (Carter, 1876; Topsent, 1892; this study); Ibero-Moroccan Gulf (Arnesen 1932; Boury-Esnault *et al.* 1994); Azores Islands (Topsent 1904; 1928; Lévi & Vacelet 1958); Canary Islands (Topsent 1928; Burton 1954); ?Philippines (Lévi & Lévi 1989).

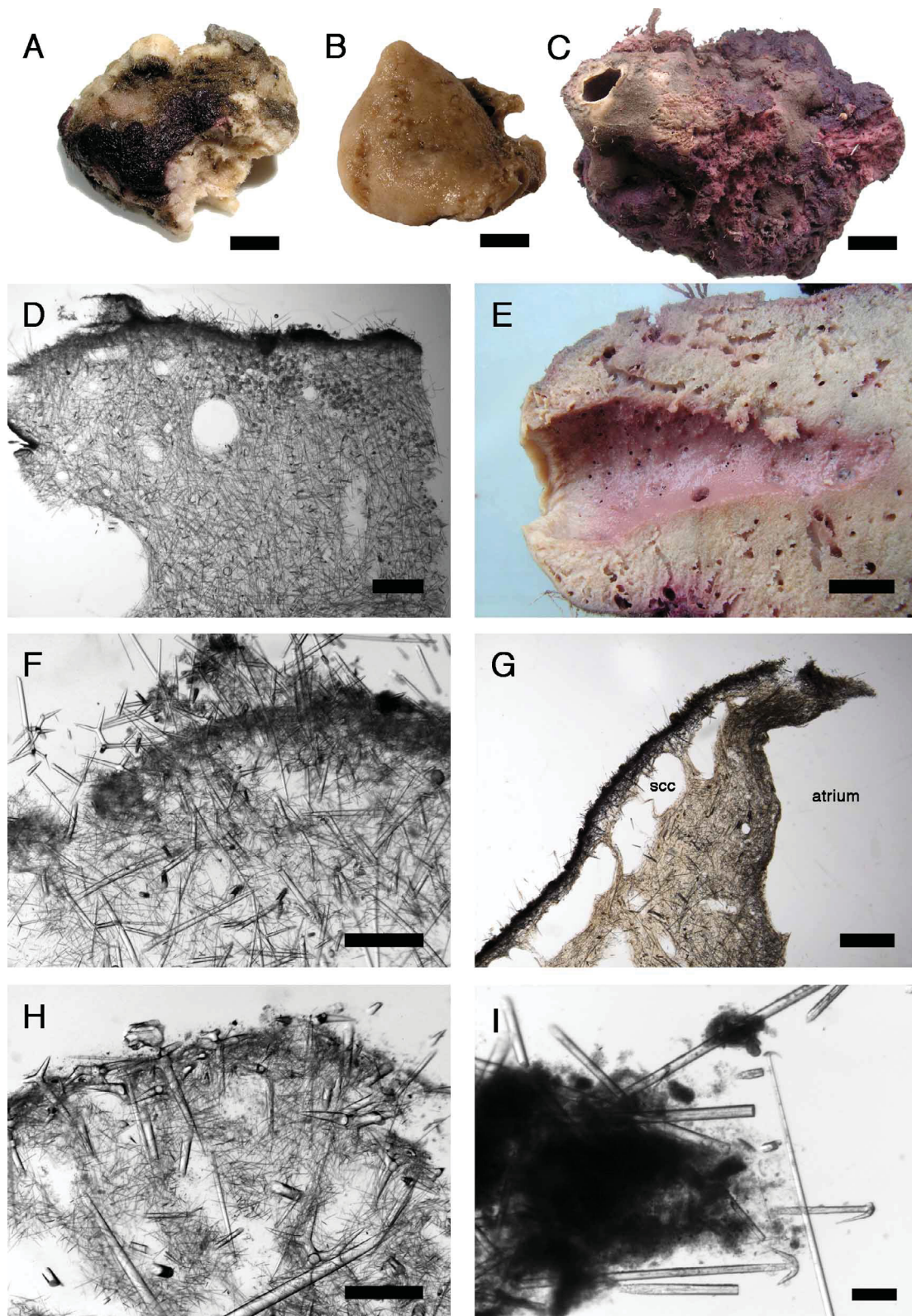


FIGURE 1. *Characella pachastrelloides* (Carter, 1876). A. ZMBN 80248 collected in Norway. Scale: 1 cm; B. ZMBN 25629 from the Ibero-Moroccan Gulf (Arnesen, 1932). Scale: 1 cm; C. ZMAPOR 20375 from Mingulay Reef, Scotland. Scale: 3 cm; D. Thick section showing the skeletal architecture of cortex and choanosome. Scale: 1 mm [ZMBN 80248]; E. Cross-section of main atrium. Notice the tough contractile membrane surrounding the oscule. Scale: 1 cm [ZMAPOR 20375]; F. Close-up of thick section D showing the arrangement of microxeas, oxeas and triaenes in the cortex. Scale: 500 μ m [ZMBN 80248]; G. Thick section of the membrane surrounding the oscule. scc: sub-cortical canals. Scale: 1 mm [ZMAPOR 20375]; H. Cross-section showing the arrangement of microxeas, oxeas and triaenes in the cortex. Scale: 500 μ m [ZMBN 25629]; I. Anatriaenes *in situ*. Scale: 200 μ m [ZMBN 85225].

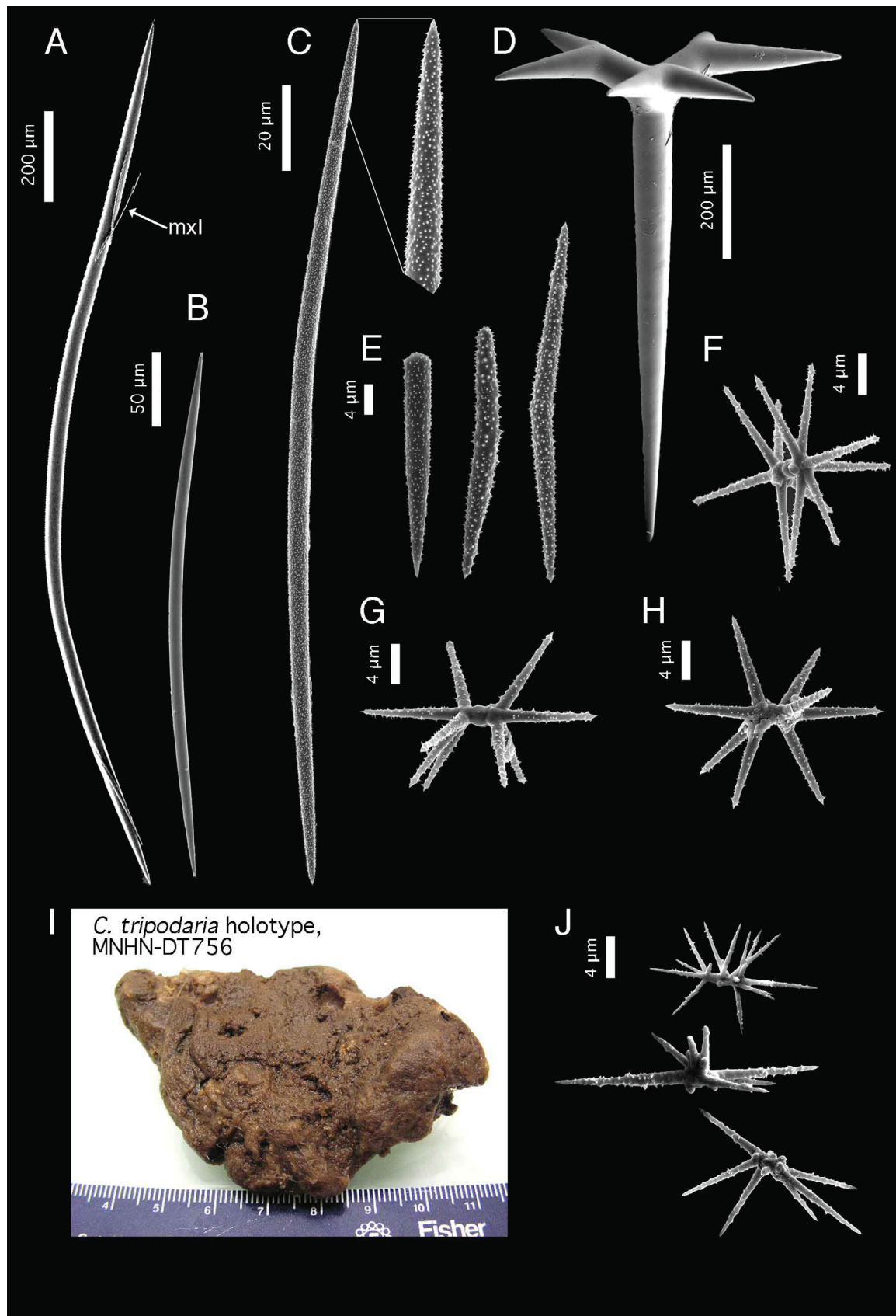


FIGURE 2. Spicules of *Characella pachastrelloides* (Carter, 1876). A. Oxea I [ZMBN 80248]. mxI: microoxea I; B. Oxea II [ZMBN 80248]; C. Microoxea I [ZMBN 80248]; D. Dichotriaene [ZMBN 25629]; E. microoxeas II [ZMBN 80248]; F. Amphiaster [ZMBN 80248]; G. Amphiaster [ZMBN 85225]; H. Amphiaster [ZMBN 25629]. *Characella tripodaria* (Schmidt, 1868) [MNHN-DT 756, holotype]. I. Whole specimen; J. Amphiasters. Notice the additional actines on the central shaft for the smaller one. Notice the underdeveloped actines and the disappearance of the central shaft on the largest one.

Depth. 140 m–1804 m (Topsent 1928; this study).

Discussion. This is the first record of *C. pachastrelloides* in Norway, which extends its distribution range to the north (Fig. 3). Our specimen was found in shallower waters than in previous records; we thus also stretch the depth range of that species. This should not come as a surprise since fjords are known to harbour deep-sea benthic organisms at shallower depths (Strømgren 1970; 1971; Fosså *et al.* 2002). It should be noted that on the Norwegian coast, *C. pachastrelloides* can easily be confused with another Astrophorida: *Stryphnus fortis* Vosmaer, 1885. They share a very similar massive morphology, with brownish hispid surfaces, large atria, and identical epibionts (e.g. encrusting sponges such as *H. dedritifera*). However, *S. fortis* has a more conspicuous cortex with larger megascleres, sanidasters (8–12 µm) and large oxyasters (50–80 µm). Also, it does not possess microxeas.

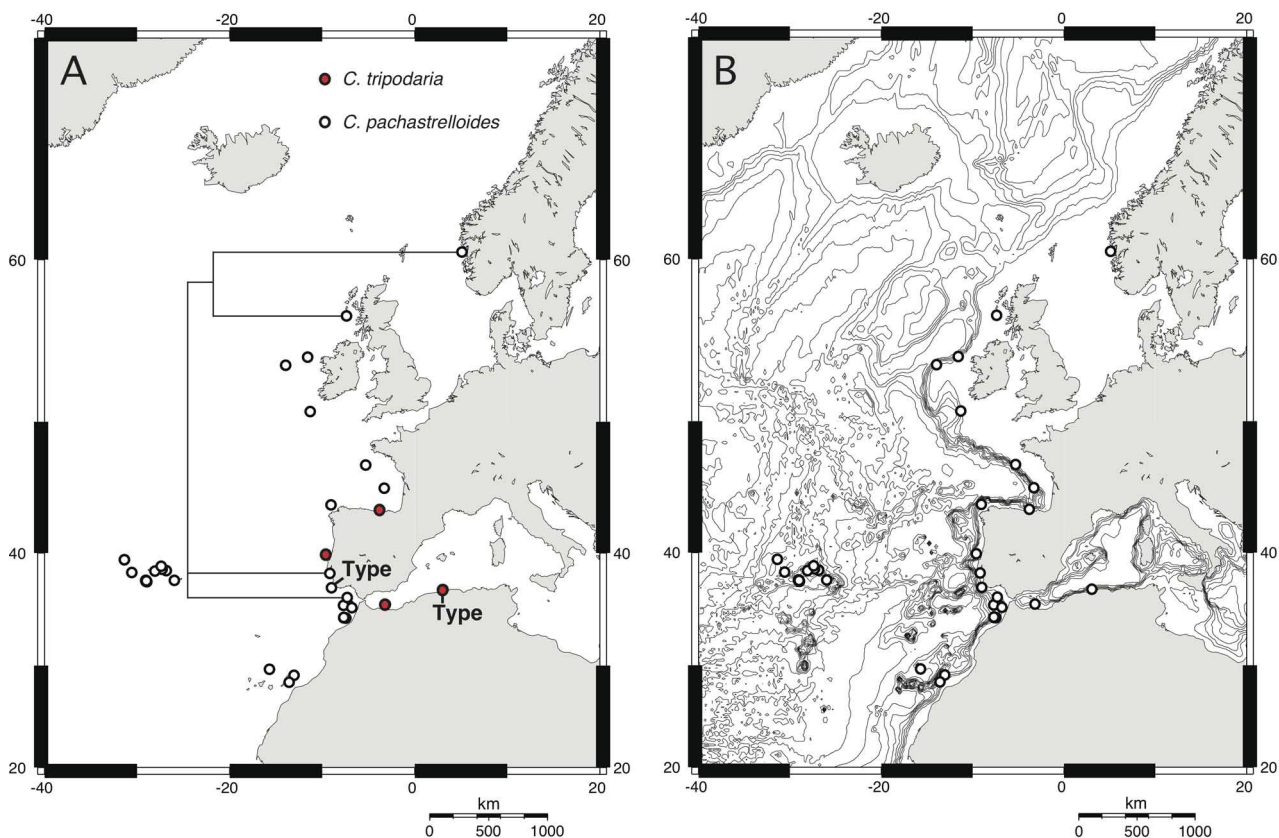


FIGURE 3. A. Geographical distribution of *Characella pachastrelloides* (Carter, 1876) and *Characella tripodaria* (Schmidt, 1868). The molecular phylogenetic tree obtained in Cárdenas *et al.* (2011) is mapped in relation with the specimens sequenced; B. Geographical distribution of *C. pachastrelloides* and *C. tripodaria* in relation with bathymetry.

Taking advantage that the Scottish specimen was nearly complete, we report here the first detailed observation of the oscule for this species. ZMAPOR 20375 was a massive lumpy specimen (17 cm high, 14 cm wide) (Fig. 1C) which had a large oscule (ca. 2 cm in diameter) placed at its summit. It is similar to a Portuguese specimen described by Topsent (1892, pl. II, fig. 3). This oscule had a tough contractile membrane around it. Other smaller oscules (0.5–0.7 cm wide) were irregularly distributed. Exhalant openings are numerous in the 10 cm deep atrium (Fig. 1E). A section in the tough contractile membrane showed that the structure of the cortex is identical to the rest of the specimen but that large sub-cortical canals appear (Fig. 1G). We have observed such canals in the cortex outside the oscule, but never in such a regular pattern.

The intra-specific variability of the spicules observed during the last revision of *C. pachastrelloides* (Maldonado 1996) is here confirmed (Table 1). Oxeas II have never been observed in this species before. Due to their rarity, we cannot rule out the possibility that these Haplosclerida-like oxeas II could in fact be foreign spicules incorporated in the choanosome. This is supported by the numerous foreign *Geodia* sterrasters observed in our sections (Fig. 1D). Only one oxea II was found in the Scottish specimen. On the other hand, these oxeas II might characterize a derived Norwegian population of *C. pachastrelloides*, but more specimens and genetic data are

needed to conclude. Also, as noted before us, *C. pachastrelloides* can either have orthotriaenes, dichotriaenes, or both (Topsent 1928; Maldonado 1996). When dichotriaenes are present, the protoclades are usually shorter than the deuteroclades. We also noticed that the morphology of the triaenes (length and width) could be quite variable between specimens (Figs. 1F, H). For example, the rhabdome of the triaenes was quite short in our Norwegian specimen (mean of 480 µm) and quite long in the Ibero-Moroccan specimens (ca 770 µm). The different environment (shallower depth, colder water) of the Norwegian specimen may explain these differences.

Maldonado (1996) acknowledges the presence of anatriaenes in the holotype (Carter 1876) and specimens from the Ibero-Moroccan Gulf (Boury-Esnault *et al.* 1994), but remains uncertain whether these are exogenous elements incorporated from the sediment. However, these same anatriaenes have been found in other specimens from Ireland (Stephens 1915), the Azores (Lévi & Vacelet 1958) and in ZMBN 85225, our sample from Portugal (Fig. 1I). In our opinion, anatriaenes were clearly not exogenous since thick sections of this specimen show them perpendicular to the sponge surface, with their cladome outside and their rhabdome crossing the cortex and the choanosome under it. They furthermore resemble the ones found in the holotype (Maldonado 1996, Figure 8c). Actually, Topsent (1892) based his description of a new species from West Portugal (*Characella sollasi*) on the absence of anatriaenes and of oxyasters (both observed in the original description of *C. pachastrelloides* by Carter). After examining slides from the Porcupine expedition (Carter 1876), Topsent (1904) later suggested that the anatriaenes and oxyasters from the holotype were probably exogenous and thus synonymized *C. sollasi* and *C. pachastrelloides*. He was right concerning the oxyasters but wrong concerning the anatriaenes. This further underlines the fact that depending on the specimens of *C. pachastrelloides*, anatriaenes can be absent or quite rare and thus easily overlooked. These were in fact not found in the Norwegian specimen.

This last result casts serious doubts on the validity of the other *Characella* species in the area: *C. tripodaria*. Records of this species are scarce (Fig. 3A) but we notice that its distribution clearly overlaps that of *C. pachastrelloides*. Spicule measurements of the holotype of *C. tripodaria* match those of *C. pachastrelloides* (Table 1). The triaenes, apparently smaller in *C. tripodaria*, are in fact similar in size to those of the Norwegian specimen of *C. pachastrelloides*. Also, we found a second category of smooth oxeas while reexamining the holotype. Topsent (1938) had considered them to be a contamination from a *Reniera* but since they also match the oxeas II found in our Norwegian specimen, they might actually belong to *C. tripodaria*. At this moment, we are unsure on the status to give to these oxeas. According to Maldonado (1996), only three differences discriminate these two species: *C. tripodaria* has (i) anatriaenes, (ii) few amphiasters and (iii) amphiasters with numerous actines (although he does not give any specific range or number). We have therefore looked at the quantity and morphology of the amphiasters present in our anatriaenes-bearing *Characella* specimens. Amphiasters in some of the specimens examined were a bit less abundant; all these specimens came from the Gulf of Cadiz (ZMBN 25628, ZMAPOR 18041, Balgim specimen). But, the amphiasters of our specimens all had 7–11 actines, versus 5–18 in the holotype of *C. tripodaria*. On average, the amphiasters of the *C. tripodaria* (holotype) clearly had extra actines (or buds of actines) on the central shaft (Fig. 2J). Underdeveloped actines were common, making the amphiasters very irregular (Fig. 2J). Often, the central shaft was shortened or missing, giving these amphiasters the appearance of euasters (Fig. 2J), which is what Carter (1876) may have observed. The amphiasters from the Alboran specimens of *C. tripodaria* had extra actines but no underdeveloped/irregular actines (Maldonado, 1996). Conversely, *C. pachastrelloides* amphiasters never had extra actines on the shaft (Fig. 2F–H), and they were all fairly regular (fully developed and always with a shaft). In our opinion, the irregular amphiasters with additional actines of *C. tripodaria* could be due to the environment and we therefore doubt the validity of *C. tripodaria*. However, consistent small differences have been shown to be of importance in sponge taxonomy and we therefore prefer to cautiously keep it as a valid species, until genetic data can settle the matter.

When we map the bathymetry over the distribution of these two species (Fig. 3B), we notice that the distribution of *C. pachastrelloides* and *C. tripodaria* perfectly follow the shelf break of the European and African continental margins. This also might explain why both species are often associated with deep-water corals (Maldonado 1996; van Soest *et al.* 2007; this study).

28S sequences were identical for all the specimens sequenced. On the other hand, we found 1 bp. difference between the COI of *C. pachastrelloides* from Norway/Scotland and *C. pachastrelloides* from Portugal/Spain (Fig. 1A). Over such a geographical distance and with such a small genetic difference, studies have shown that sponge species can be cryptic (Cárdenas *et al.* 2007), but in our case, no clear morphological difference justifies the splitting of *C. pachastrelloides* into a northern and a southern NEA species.

TABLE 2. Individual spicule dimensions for specimens of *Characella pachastrelloides* and *Characella tripodaria* (in µm) with dimensions of the specimens. Means are in bold; other values are ranges; n = 30 unless stated otherwise between parentheses. - = not referred; n.f. = not found in this study.

Material	Depth (m)	amphiaser (length)	Microxea I (length/width)	Microxea II (length/width)	Triaxene rhabdome (length/width)	Orthotriaenes (clads) or dichotriaenes (protoclade + deuterooclade)	Oxeas I (length/width)	Oxeas II (length/width)	Anatriaenes (length/width/clads)
<i>Characella pachastrelloides</i> ZMBN 80248 * Hjeltefjord, Norway	80-140	13- 18.1 -29	80- 194.9 -259/ 2- 4.4 -5	24- 35.2 -49/ 2- 2.6 -4	168- 407.8 -630/ 11- 32.6 -49	83- 175.1 -316 (18) (orthotriaenes) 70- 98.8 -129 + 72- 135.6 -194 (12) (dichotriaenes)	1210- 1769.1 - 2184/ 20- 37 -52	300- 381.4 -438/ 9- 11.7 -13 (21)	n.f.
Cape St. Vincent, Portugal holotype (Sollas 1888; Maldonado 1996)	683	13	245/ 6.4	46.5/ 8.5	850/ 70	490 (orthotriaenes)	3660-4620/ 84-100	-	3660-6640/ 21/ 100-170 (rare) n.f.
West of Portugal (Topsent 1892)	300-736	20	200-220/ -	35-40/ -	-	- (orthotriaenes)	2500-3200/ -	-	n.f.
ZMBN 85225 * Setúbal canyon, Portugal	1393	13- 21.0 -39	155- 219.7 -287/ 4- 5.0 -6	20- 31.0 -39/ 3- 3.0 -3	540- 827.9 -1052/ 51- 66.4 -81 (N=17)	428- 721.4 -1026 (N=15) (orthotriaenes)	Up to 3000/ 30- 49.5 -85 (10)	n.f.	2750- 2901 -3052 (2)/ 20- 27.4 -30 (10) / 61- 145.2 -204 (10) n.f.
ZMBN 25629 * Ibero-Moroccan Gulf (Amesén 1932)	1215	13- 16.4 -25	166- 242.9 -290/ 5- 5.0 -7	26- 33.5 -44/ 2- 2.0 -2	489- 769.7 -1020/ 31- 62.4 -90	102- 141.9 -193 + 90- 215.7 -306 (dichotriaenes)	1578- 2672.1 - 3025/ 40- 70.4 -100	n.f.	-/ -/
Ibero-Moroccan Gulf (Boury-Esnault <i>et al.</i> 1994)	948-1515	12- 20 -25 (rare)	175- 216 -260/ 4- 4.6	32- 20 -50/ 4-5	580- 770 -950/ 55- 68 -75	480- 534 -560 (ortho- and dichotriaenes)	2100- 2537 -2980/ 50- 61 -70	-	105-115 (rare) n.f.
Azores Islands (Topsent 1904)	523-845	(rare)	-	Up to 40/ -	Up to 500-800/ -	110 + 230-280 (ortho- and dichotriaenes)	3000-4000/ -	-	-
Azores Islands (Lévi & Vacelet 1958)	370-460	13-14 (rare)	110-275/ 4-7	20-25/ 2-3	550/ 17	550 (orthotriaenes)	1600-2750/ 45	-	-/ -/
<i>Characella cf. pachastrelloides</i> Manila, Philippines (Lévi & Lévi 1989) except * <i>Characella tripodaria</i> BNHM: 68.3.2.36 Algeria holotype (Maldonado 1996) except *	170-520	25-30	90-210/ 3-6	25- 32.6 -38/ 3- 4.1 -4.5 (10)* 35-45/ 1.5-2.5	200-600/ 20-75 180-400/ 15-22	170-500/ 20-70 (orthotriaenes)	1500-3000/ 25-100	n.f.	110 (rare) n.f.
Alboran Island (Maldonado 1996)	70-120	10-17 (rare)	121-243/ 3-5	30-50/ 2-4	200-524/ 25-30	180-400 (orthotriaenes)	1000-1600/ 10-40	267- 343.6 -406*/ 5-7.0-10* foreign?	-/ 10/ 25
						200-524 (orthotriaenes)	900-2430/ 20-58	-	1300-3000/ 9-19/ 20-75

* spicules measured for this study.

We have re-examined the specimen identified as *Poecillastra sollasi* (ZMAPOR 5300) from the Barbados (van Soest & Stentoft 1988). It has a clear plate-like morphology, clearly different from the massive *C. pachastrelloides*. Its calthrop-like triaenes are significantly smaller than the NEA triaenes of *C. pachastrelloides*. Also, its microscleres are very different from *C. pachastrelloides*: (i) most of its microxeas are conspicuously centrotylote, (ii) the streptasters are mainly plesiasters (sometimes modified to amphiasters) and few metasters-spirasters, (iii) plesiasters are very large (diameters of 60 μm are common, and we observed sizes up to 100 μm). *Poecillastra dilifera* (holotype USNM 22331) from the Puerto-Rico trench has a very similar external morphology to the Barbados specimen. However, a comparison with a slide of the paratype of *P. dilifera* (MNHN-DNBE1) showed that *P. dilifera* had (i) only one size of microxea, of length 77.5–178.3–262 μm (vs. two sizes: 155–220 μm and 36–60 μm in the Barbados specimens), (ii) much thicker microxeas, width 2–4.8–7.5 μm (vs. 2–5 μm), (iii) much more spirasters and (iv) smaller plesiasters, diameter of 23–38 μm . For these reasons, we temporarily consider the Barbados specimens different from *P. dilifera*. The Barbados specimens are atypical because they possess simultaneously *Characella* characters (two size categories of microxeas) and *Poecillastra* characters (spirasters and metasters, plate-like external morphology). Both genera have been shown to be phylogenetically quite distinct and it has been suggested to prioritize the morphology of the streptasters (amphiasters vs. spirasters-metasters-plesiasters) to better separate these genera (Cárdenas *et al.* 2011). Until a comprehensive revision of these genera is made, the Barbados species is named *Poecillastra* sp. We suspect this species to be new but a comprehensive revision of western Atlantic *Poecillastra/Characella* species is required, a task beyond the purpose of our study.

Characella tuberosa from Durban (South Africa), synonymized with *C. pachastrelloides* by Lévi & Lévi (1989), is actually fairly different. *C. tuberosa* (MNHN-DCL 1396) had a few spirasters mixed with a majority of amphiasters. These spirasters are never present in *C. pachastrelloides*. We therefore propose to resurrect *C. tuberosa* as a valid species until further specimens from South Africa can be examined. We also stress that this species should remain in the *Characella* genus since it has two sizes of microxeas and amphiasters as the main streptaster. *Characella flexibilis* Lévi, 1993 from New Caledonia is also fairly close to *C. pachastrelloides* but is discriminated by its cup/blade morphology and its elasticity (Lévi 1993). On the other hand, we re-examined specimens and slides (MNHN-DCL3228–3229) of the *C. pachastrelloides* collected in Manila (Philippines) (Lévi & Lévi 1989). The only difference with our NEA specimens is slightly wider microxeas II: they were 3–4.1–4.5 μm (N=10, MNHN-DCL3229) whereas the ones we measured in the NEA specimens were on average thinner than 3 μm (Table 2). Genetic data is now needed to investigate if this is a cryptic species, different from *C. pachastrelloides*, as suggested by its remote geographic location.

Family Pachastrellidae Carter, 1875

Diagnosis: Astrophorida with a majority of amphiasters as streptasters (never spirasters) in combination with large calthrops and/or short-shafted mesotriaenes or mesotrider desmas. A variety of monaxonic spicules can be present: microxeas, microrhabds, microstrongyles and microrhabdose streptasters (Cárdenas *et al.* 2011).

Genera: *Brachiaster*, *Nethea*, *Pachastrella*, *Triptolemma*.

Genus *Pachastrella* Schmidt, 1868

Diagnosis: Pachastrellidae with large four rayed clathrops (never becoming mesotrider desmas). Microscleres always include microstrongyles.

Pachastrella nodulosa sp. nov.

(Figures 4–10, Table 3)

Synonymy.

Pachastrella monilifera: Burdon-Jones & Tambs-Lyche 1960, p. 6; Koltun 1966, p. 30.

Pachastrella sp.: Cárdenas *et al.* 2011, Table S1.

Not *Pachastrella monilifera* Schmidt, 1868: Schmidt, 1868, p. 15.

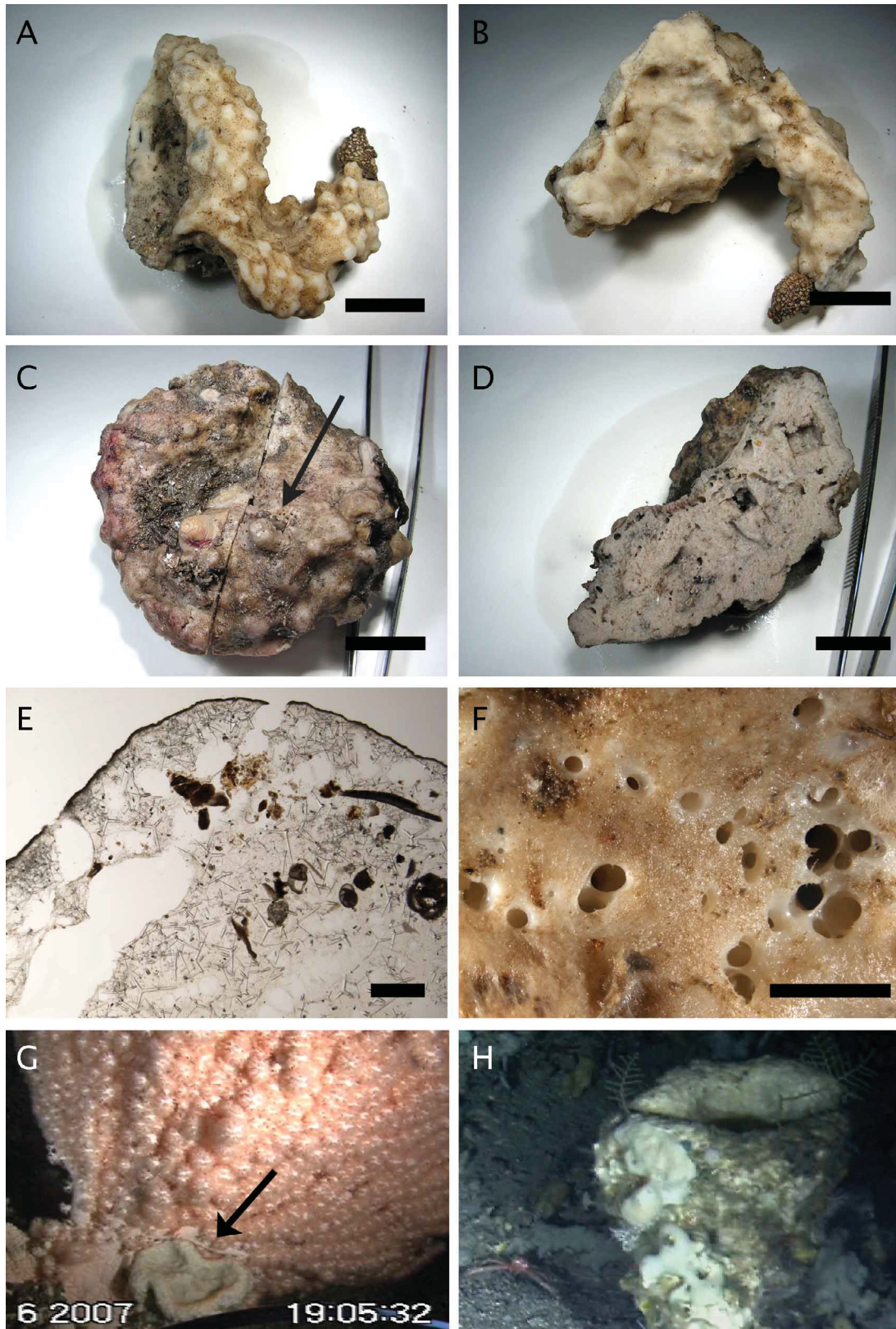


FIGURE 4. *Pachastrella nodulosa* sp. nov. A. Whole specimen, top knobby surface. Scale: 3 cm [ZMBN 85243]; B. Whole specimen, under surface. Scale: 3 cm [ZMBN 85243]; C. Holotype, top knobby surface. Arrow points at oscule area. Scale: 2 cm [ZMBN 85242]; D. Cross-section of holotype showing the dense choanosome. Scale: 2 cm [ZMBN 85242]; E. Thick section of oscule area. Scale: 1 mm [ZMBN 85242, holotype]; F. Oscules. Scale: 5 mm [ZMBN 85244]; G. Specimen *in situ* (arrow) at the base of *Paragorgia arborea* (Linnaeus) as seen from the manned-submersible JAGO, Trænadjupet, northern Norway, 298 m. Specimen is approximately 30 cm in size; H. Specimen *in situ* as seen from the manned-submersible JAGO, Trænadjupet, northern Norway, 301 m. Specimen is approximately 20 cm in diameter.

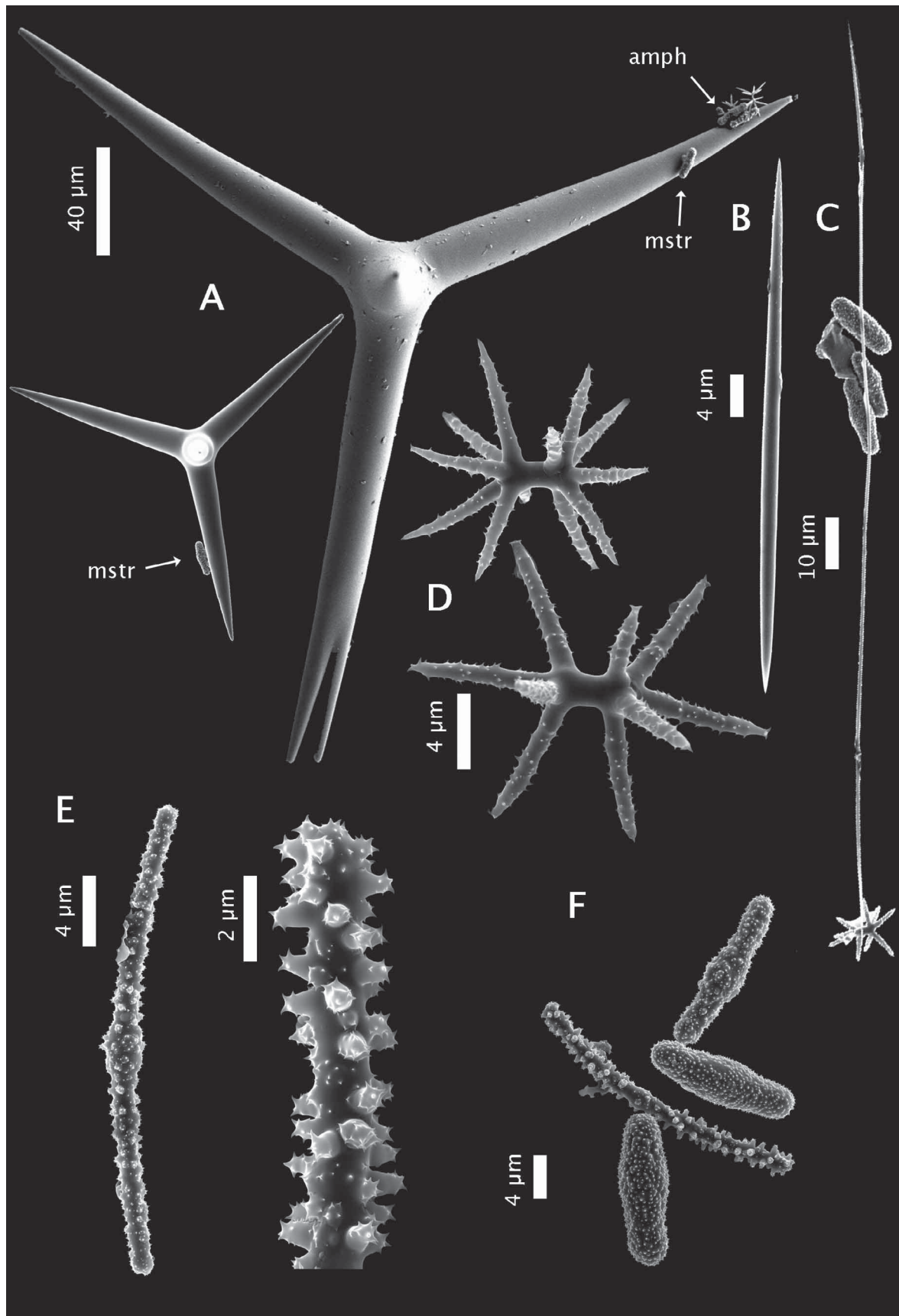


FIGURE 5. Scicules of *Pachastrella nodulosa* sp. nov. [ZMBN 85242, holotype]. A. Large and small calthrops. mstr: microstrongyles. amph: amphistars; B. Microstrongyle; C. Microstrongyle (whip-like), foreign?; D. Amphistars; E. Microrhabdose streptaster and detail; F. Microstrongyles and microrhabdose streptasters.

Type series. ZMBN 85242, holotype, Steinneset, Langenuen, western Norway, 59°53'N, 05°31'E, depth: 25–175 m, triangular dredge; ZMBN 85227, 85243, paratypes, Skorpeodden, Korsfjord, western Norway, 60°10'N, 05°10'E, depth: 200–400 m, triangular dredge; ZMBN 85244, paratype, Røst Reef, northern Norway, 67°30'N, 9°24'E, depth: 282–290 m, manned-submersible; ZMBN 85245, paratype, Trænadjupet, northern Norway, 66°58'N, 11°7'E, depth: 316 m, manned-submersible.

Additional material examined. NTNU-VM 54998, northern Norway.

Comparative material examined.

Pachastrella monilifera, MNHN-DT410, holotype, coast of Algiers.

Pachastrella abyssi Schmidt, 1870, MZS P0195, holotype, dry, Florida; *Pachastrella* cf. *abyssi*, HBOI 198811141008, off Savannah, Georgia, U.S.A., 31°41'N, 79°08'W, 533 m, det. P. Cárdenas; ZMAPOR 05301, dry, off Payne's Bay, Barbados, 153 m (van Soest & Stentoft 1988).

Pachastrella ovisternata von Lendenfeld, 1894, MNHN-DCL4065, Portugal, det. M. Maldonado.

Pachastrella sp. 1, originally identified as *P. monilifera* (Lévi 1967), MNHN-DCL680L, 681, 691, slides, South Africa, 47–130 m, det. P. Cárdenas.

Pachastrella sp. 2, originally identified as *P. monilifera* (Lévi & Lévi 1989), MNHN-DCL3372, slides, off Lubang Island, Philippines, MUSORSTOM 1, 14°01'N, 120°16'E, 183–185 m, det. P. Cárdenas.

Outer morphology (Fig. 4). Massive irregular or cup-shaped (ZMBN 85242, ZMBN 85243). Large specimens (ca 20 cm high and 25 cm wide) observed with the manned-submersible were usually cup (Fig. 4G–H) or half-cup shaped with a deep or shallow central depression. Surface and choanosome color is whitish or yellowish-cream to dark brown (alive and in ethanol). Specimen is slightly compressible. Surface is very rugose, as sandpaper. Choanosome is dense and also rugose (due to the abundance of calthrops). Upper and side surfaces around the central depression are knobby (each knob with a diameter of 0.5–1 cm) while the lower surface is more irregular. Small oscules are grouped in the oval to circular depressions on the upper surface (Fig. 4F), where knobs are absent. Each oscule has a diameter of 0.5–1.5 mm. Pores are not visible. Cortex is not conspicuous. Macroepibionts include bivalves, polychaetes, ascidians, hydroids, sea anemones, pycnogonids, and other sponges (e.g. *Cyamon spinispinosum* (Topsent, 1904), *Hexadella dedritifera*).

Skeleton (ZMBN 85242) (Fig. 4E). Thin cortex of microstrongyles (36–73 µm thick). Calthrops (with no particular orientation), microstrongyles and abundant amphiasters fill the choanosome. Microstrongyles are also found lining the canals. Foreign material and spicules are abundant (e.g. sigmas, discorhabds and tylotes).

Spicules (ZMBN 85242) (Fig. 5). (a) calthrops, few dichotomous actines, actine length: 47–244.3–768 µm; actine width: 4–28.7–73 µm. (b) microxeas, rare, smooth length: 44.8–91.1–190 µm; width: 0.7–2.0–2.5 µm (N=26). The longest of these microxeas (109–190 µm) seemed thinner (0.7–0.9 µm), almost whip-like and may represent a separate category of microxeas, or be foreign, only six were found. (c) microstrongyles, in high numbers, microspiny, straight, centrotylote or not, length: 13.6–15.7–26 µm; width: 3.1–4.7–5.8 µm. (d) microrhabdose streptasters, rare, straight or slightly bent, sometimes centrotylote, length: 23–30.3–34.7 µm; width: 1.4–2.1–2.6 µm (N=7). (e) amphiasters, ca. 5–11 actines (usually 5 actines on each end of the naked shaft, actines often have a tip with two spines), microspiny, length: 10.8–14.8–22.6 µm; width: 7–11.5–17.5 µm.

Distribution (Fig. 6). Norwegian Sea and Norwegian coast (Burdon-Jones & Tambs-Lyche, 1960; Koltun, 1966; this study).

Depth. 25–400 m.

Discussion. *P. nodulosa* is a fairly common species in Norway. During a three-hour dive in Trænadjupet (northern Norway) with the manned-submersible JAGO, we spotted more than a dozen large specimens (Fig. 4G–H). *Pachastrella* species can be difficult to discriminate and since *P. monilifera* was the first species of this genus to be described, many records from the Atlantic and Pacific have excessively used that name. Kirkpatrick (1902) and von Lendenfeld (1907) were among the first authors to discriminate new species from the *P. monilifera* complex. According to the latest revision (Maldonado 2002), there are three *Pachastrella* species in the NEA: *P. monilifera*, *P. ovisternata* and *P. chuni*. Upon collection, the Norwegian specimens were initially identified as *P. monilifera*, following previous Norwegian records (Burdon-Jones & Tambs-Lyche 1960; Koltun 1966). However, *P. nodulosa* differs from the *P. monilifera* holotype (Fig. 7A–B) by (i) its knobby surface, (ii) the absence of large oxeas (noticed by Koltun (1966)), (iii) its amphiasters have on average less actines and these are less spiny, and finally (iv) differs morphology and rareness of the microxeas. Fairly common in *P. nodulosa*, microrhabdose streptasters were not found in the holotype of *P. monilifera*. This was not considered to be a difference since they can be quite

rare, and they have been observed in other Mediterranean specimens (Table 3). *P. nodulosa* is also different from *P. ovisternata* (Fig. 7C–D) and *P. chuni* for the same reasons as for *P. monilifera*, and also because of the absence of small dichotriaenes (*P. ovisternata* and *P. chuni*) and mesodichotriaenes (*P. ovisternata*) in the choanosome. We however note that a knobby surface has also been observed in *P. ovisternata* (M. Maldonado, pers. com.) so this character may not be unique to *P. nodulosa*. Interestingly, the morphologies of the largest category of calthrops were somewhat characteristic in each NEA species: often plagiotriaene-like with stout regular actines in *P. monilifera* (Fig. 10A); plagiotriaene-like or not, with thinner regular actines in *P. nodulosa* (Fig. 10B); and often irregular actines in *P. ovisternata* (Fig. 10C) or *P. chuni*. The morphology of the large calthrops seems to be consistent: large calthrops from drawings of Mediterranean *P. monilifera* are very similar to what we observed in the type (Topsent 1894; Babiç 1922). The last species of the Atlanto-Mediterranean area, *Pachastrella echinorhabda* Pulitzer-Finali, 1972 from the Mediterranean, has characteristic acanthorhabds, absent in all other Atlantic species, including *P. nodulosa*.

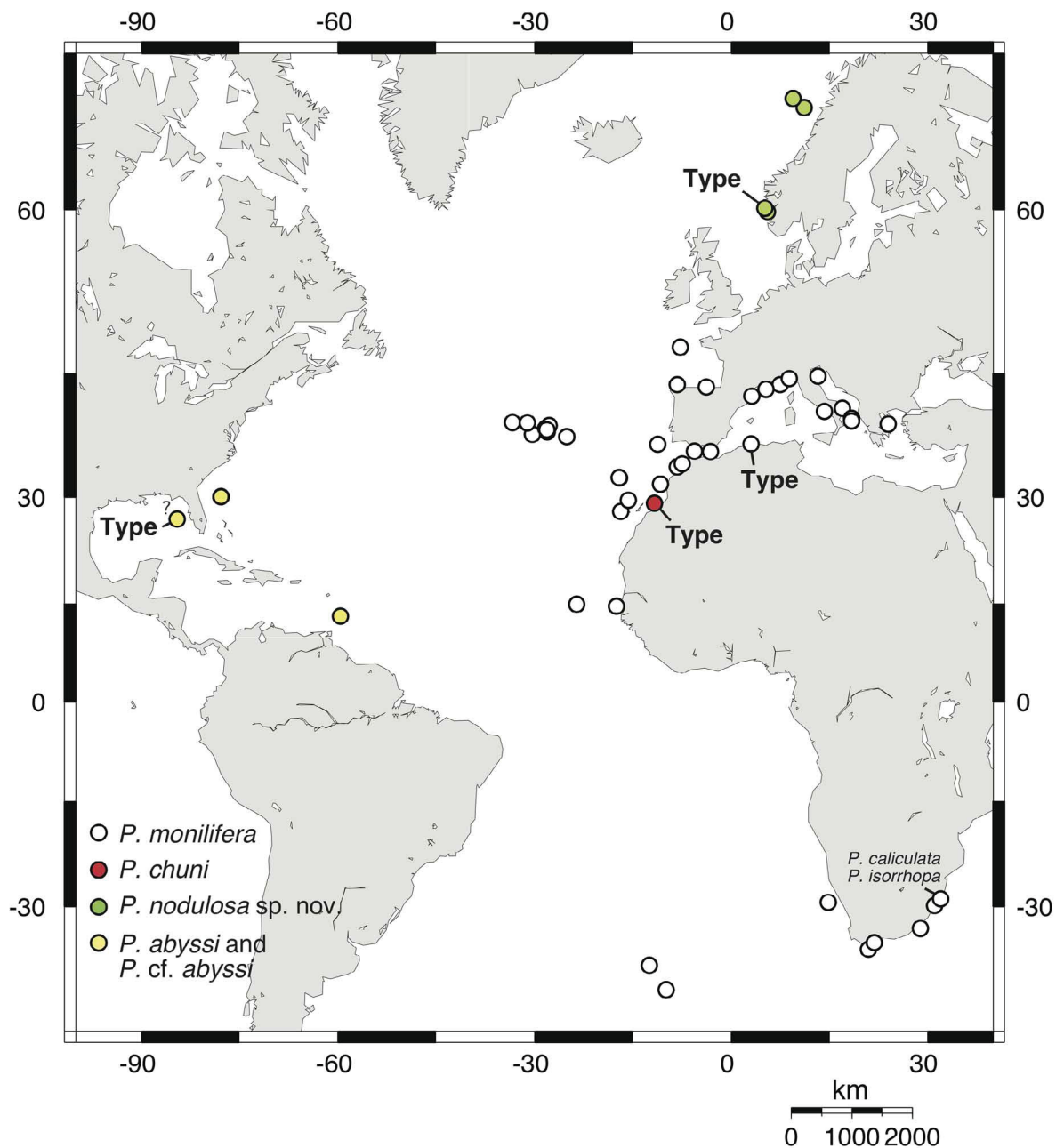


FIGURE 6. Geographical distribution of *Pachastrella abyssi* Schmidt, 1870, *Pachastrella chuni* Lendenfeld, 1907, *Pachastrella monilifera* Schmidt, 1868, and *Pachastrella nodulosa* sp. nov. in the Atlantic Ocean.

TABLE 3. Depth, shape and individual spicule dimensions (in µm) for specimens of *Pachastrella*. Means are in bold; n.f. = not found; n=30 unless stated otherwise between parentheses. - = not referred; n.f. = not found in this study.

Material	Depth (m)	Shape	Oxeas (length/width)	Small dichotriaenes	Actine of caltrop (length/width)	Microxeas I (length/width)	Microxeas II (length/width)	Microhabds (length/width)	Microhabdose streptasters (length/width)	amphiasier (length/width)
<i>Pachastrella nodulosa</i> ZMBN 85242*, holotype Western Norway	25-175	Massive shallow cup, knobby surface	n.f.	no	47- 244.3 -768/ 4- 28.7 -73	44.8- 91.1 -190/ 0.8- 2.0 -2.5 (11)	n.f.	13.6- 15.7 -26/ 3.1- 4.7 -5.8	23-30.3 -34.7/ 1.4- 2.1 -2.6 (7)	10.8- 14.8 -22.6/ 7- 11.5 -17.5
ZMBN 85227*, paratype Western Norway	200-400	Massive irregular, knobby surface	n.f.	no	23- 294.7 -864/ 2.5- 27.6 -76	306- 315.4 -321/ 5- 8.0 -10 (7)	n.f.	7- 13.1 -20.5/ 2.5- 4.0 -6.5	20.5- 28.4 1/ 1.5- 1.9 -2.2 (16)	9- 13.9 -20.5/ 6.5- 9.2 -11.5
<i>Pachastrella monilifera</i> Algeria MNHN-DT410*, holotype	?	Massive, fragment	1584- 2488 -3264/ 18- 23.3 -33 (N=6)	no	51- 318.4 -1008/ 7- 41.9 -129	226- 264.9 -292/ 3- 5.9 -9	109- 150.4 -186/ 2- 3.7 -4.5	11.5- 13.7 -16/ 2- 2.4 -3.5	n.f.	7.8- 11.1 -15.5/ 6.6- 8.7 -12.5
Naples, Italy (Pulitzer-Finali 1972)	40-120	- Irregular - incrusting	Up to 1600/10 Up to 3000/30	no	Up to 550/- Up to 400/-	110-240/5-7 160-190/-	-	12-18/1.5-2.5 14-5/5	n.f. 35/1-1.5	12-18/ 12
Ibero-Moroccan Gulf (Boury-Esnault <i>et al.</i> 1994)	550-948	Irregular, incrusting	1900- 2525 -3050/ 18- 22 -26	no	150- 373 -680/ 12- 46 -80	-	-	12- 17 -21/ 4-7-10	-	12- 24 -30/ -
Gorringe Bank (Lévi & Vacelet 1958)	95	Massive irregular	1100-1200/-	no	100-650/ 75	-	-	15/ -	-	10-11/ -
<i>Pachastrella ovisternata</i> Cape Finisterre, Spain (Maldonado 1993)	300	Massive irregular, slight knobby surface	3600-7500/ 16-45	yes	122-1100/ 8-55	yes (Maldonado, 2002)	-	12-19/ 5-9 (rarely centrotyle)	25-45/ 1-2 (rare)	17-22/ -

... Continued on next page

TABLE 3. Continued.

Material	Depth (m)	Shape	Oxeas (length/width)	Small dicho- triaeas	Actine of calthrops (length/width)	Microxeas I (length/width)	Microxeas II (length/width)	Microtrahabs (length/width)	Microtrahabose streptasters (length/width)	amphiaster (length/width)
<i>Pachastrella chuni</i> Western Sahara, holotype (von Lendenfeld 1907)	146	Irregular, sub-spherical and flattened	2000-5100/ 16-32 (some styles)	yes				12-17/ 3-5	13-37/ 0.5-2.5	8-21/ 11-21
<i>Pachastrella</i> sp. Namibia (Uriz 1988)	245	Massive, flat	3200/ 30	no	100-1200/ 8-89	-	-	12-18/ 5-6	110-120/ 2 (not centrotrolyote)	12-20/ -
<i>Pachastrella</i> sp. Gough Island (Topsent 1913a)	183	Massive	2000-3000/ 15	no	35-600/ 2-60	-	-	14/ 5	-	12-14/ -
<i>Pachastrella</i> sp. Tristan da Cunha (Sollas 1888)	200	Plate-like irregular mass	2540/ 16	no	796/ 63.6	-	-	14/ 4.6	83 (contami -nation?)	11.8-15.8/ -
<i>Pachastrella abyss</i> Florida MZS PO195*, holotype	417?	Irregular cup shape	2870-3250.3- 3720/ 22-33.3-40 (6)	yes	40-397.2- 1152/ 3.5-54.0-143.4	98-182.5-232/ 4.5-10.3-15.7 (smooth)	n.f.	7.2-18.1-43.2/ 2.6-5.7-7.9 (rarely centrotrolyote)	19.5-32.6-45.1 (19)/ 1.3-2.0-3.0	12.1-14.5-17.6/ 8.5-11.5-15 (spirasters, amphiasters)
<i>Pachastrella</i> cf. <i>abyssi</i> Off Georgia, U.S.A. HBO1 198811141008*	533	Plate-like	1350-2129- 2600 (6)/ 12.5-23.5-40 (14)	no	75-336.0-800/ 10-51.6-120	125-140.0-165/ 2-3.1-5 (centrotrolyote, rough)	n.f.	8-12.7-23/ 3-5.4-8 (rarely centrotrolyote)	14-30.6-47/ 2	8.5-12.1-16/ 7.5-10.1-14 (spirasters, amphiasters)
<i>Pachastrella</i> cf. <i>abyssi</i> Barbados ZMAPOR 05301/05312 (van Soest & Stenotft 1988)	153	Irregular cups, cylinders or plate-like	2000/ 25-40	no	60-650/ 5-115	142-195.1-223/ 3-5.4-7 (10) ^a (smooth)	n.f.	8-11.7-17.5/ 1.5-2.8-5 ^a (usually centrotrolyote)	30-35/ 1	15-26/ -
<i>Pachastrella</i> sp. Philippines MNH-DCL3372 (Lévi & Lévi 1989)	183- 185	Cup	2000-3500/ 50-100	yes	80-1500/ 40-200	-	-	15/ 7	-	15 (spirasters, amphiasters)

* spicules measured for this study.

^a spicules from ZMAPOR 05301 measured for this study

By identifying *P. nodulosa*, our study further confirms the existence of a *P. monilifera* species complex and thereby shows how necessary a comprehensive revision of *P. monilifera* and its many synonyms is. This is beyond this study, but our observations have nonetheless led to a few taxonomical conclusions that could initiate this sizeable work. As shown above, skeleton organization and large calthrops morphology has been shown to be useful to discriminate species, we recommend their usage to reassess the status of *Pachastrella* species.

P. abyssi from Florida has been synonymized with *P. monilifera* (Topsent 1894), but occurrence of the same sponge species on both sides of the Atlantic was considered suspicious, so we re-examined the holotype (Figs. 7E-F; 9). It has a plate-like shape (Fig. 7E), similar to the shape of *P. monilifera* (Bo *et al.* 2012). But the microscleres observed in the holotype of *P. abyssi* (Fig. 9B-I) are quite different from the ones of *P. monilifera* and *P. nodulosa*. First of all, we observed a few meso/dichotriaenes in our spicule preparations of the holotype (rhabdome: 32-50.5-75 x 4-7.7-10 µm (N=4); protoclade + deuteroclade: 20-31.7-55 µm + 15-27.3-55 µm (N=17)), similar in size and shape to the ones found in *P. ovisternata*. These meso/dichotriaenes are absent in *P. monilifera*. Furthermore, compared to *P. monilifera*, the microstrongyles in *P. abyssi* are more “chubby” and consequently less centrotylote; some can also be fairly elongated, but they are not common (Fig. 9G). The amphiasters have on average more actines, some of which can even be placed on the shaft (which is usually naked in *P. monilifera* and *P. nodulosa*); the shaft can occasionally be bent and therefore some of these strepasters could be called spirasters (Fig. 9D-E). We also noticed some very small sanidaster-like amphiasters with numerous actines (Fig. 9F); these are not common but they were never observed in the other *Pachastrella* species examined. Moreover, in the holotype of *P. abyssi* (Fig. 9B-C) microxeas are clearly thicker (Table 3) than in *P. monilifera* (Fig. 8B-C). We could also distinguish two size classes of microxeas in *P. monilifera*, against only one in *P. abyssi*, *P. chuni* and *P. nodulosa*. These microxeas are common in *P. abyssi*, *P. chuni* and *P. monilifera* but rare (or even foreign?) in *P. nodulosa*. Microrhabdose strepasters are common in *P. abyssi* and *P. nodulosa*, they are rare in *P. monilifera*. Finally, the large calthrops are regular, rarely bent, and very stout which makes them different from those of the other species (Fig. 10). It is therefore quite clear that the holotype of *P. abyssi* is different from *P. monilifera*, *P. chuni* and *P. nodulosa*: it should be considered as a valid species. However, *P. abyssi* remains a poorly known species and after examining two other *Pachastrella* cf. *abyssi* specimens from the North-western Atlantic we are still unsure about the relevance and variability of some characters observed in the holotype of *P. abyssi*. The Barbados specimen of *P. cf. abyssi* (ZMAPOR 0531) matched the holotype, except for four observations. The microxeas, which had been overlooked by van Soest & Stentoft (1988), are slightly thinner than in the holotype (Table 3). The microstrongyles are smaller (Table 3), not “chubby” and consequently more centrotylote. We could not find meso/dichotriaenes, but even in *P. ovisternata*, these can be absent from certain parts of the sponge. We also noticed that ZMAPOR 0531 had only large styles and strongyles instead of oxeas; but this may be just intra-specific variation since the large calthrops often had blunted actines (often shortened) and since van Soest & Stentoft (1988) observed oxeas in other Barbados specimens. The Georgia specimen (HBOI 198811141008) shared most characters with *P. abyssi* including the presence of spirasters and sanidaster-like strepasters. But it also differed from the holotype regarding the microxeas: it had smaller microxeas that are centrotylote and rough (vs. larger smooth non-centrotylote in holotype). It seems like an important difference but we have examined too few specimens to conclude whether HBOI 198811141008 could be a different species at this point. We could not find meso/dichotriaenes in HBOI 198811141008 either.

We have examined additional material identified as *P. monilifera*, from South Africa (MNHN-DCL680, 681, 691). Once again, we found it slightly different from all the other Atlantic *Pachastrella*. It is characterized by i) large calthrops with frequent bent actine tips, ii) smaller and more compact microstrongyles. This material should be carefully compared with the holotype of *Pachastrella caliculata* Kirkpatrick, 1902 (a synonym of *P. monilifera*) in order to eventually propose the resurrection of this South African species. We have also re-examined *P. monilifera* from the Philippines (MNHN-DCL3372, 3373). In our opinion, i) the very large oxeas and calthrops (with irregular branching actines) and ii) the small dichotriaenes (as in *P. chuni* and *P. ovisternata*) clearly discriminate it from *P. monilifera*. Further studies are needed to say if it represents a new species.

Many species described in the *Pachastrella* genus actually lack the characteristic microstrongyles and amphiasters, which make us believe they should be moved to the genus *Poecillastra*: *Pachastrella cribrum* Lebewohl, 1914, *Pachastrella fusca* Lebewohl, 1914, *Pachastrella incrustata* Bergquist, 1968, *Pachastrella scrobiculosa* Lebewohl, 1914. A re-examination of the type of *Pachastrella multipora* Dickinson, 1945 will be necessary to take a decision, notably because this species has lost its monaxonic microscleres. Southern Atlantic

and Antarctic specimens, until now also identified as *P. monilifera*, are also in need of a revision to confirm their status (Table 3). All in all, we consider seven species of *Pachastrella* to be valid (*P. abyssi*, *P. chuni*, *P. echinorhabda*, *P. monilifera*, *P. nodulosa* sp. nov., *P. ovisternata*, and *P. loricata*), while *P. multipora* and several *Pachastrella* sp. await confirmation of their status (Table 3). These results illustrate once more how thorough reexamination of a cosmopolitan species (*P. monilifera*) can reveal a species complex. Following this, further identifications and synonyms of *P. monilifera* (and *P. ovisternata*) from remote geographical locations (especially from the Indian and Pacific Ocean) should be considered with caution.

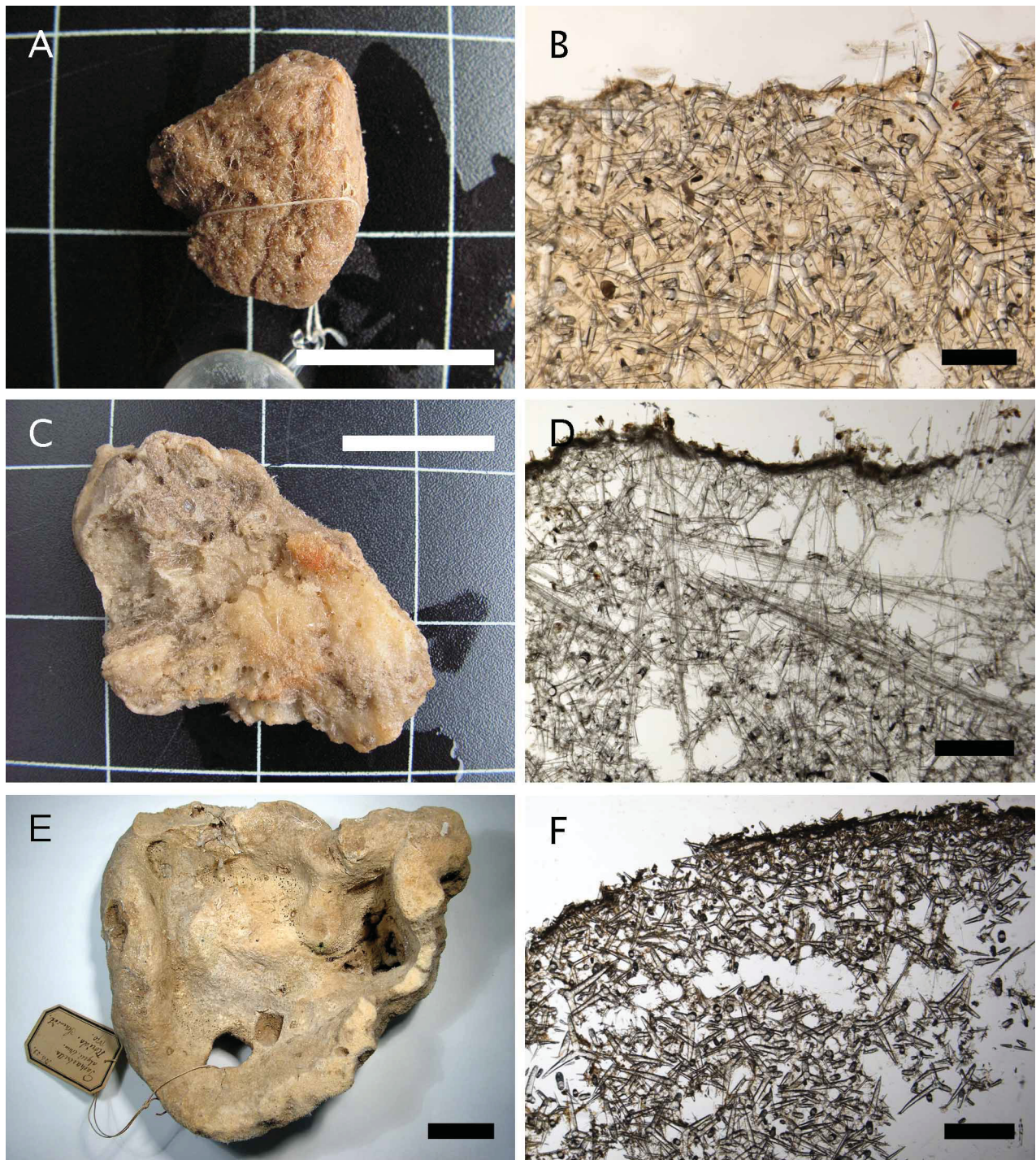


FIGURE 7. *Pachastrella monilifera* Schmidt, 1868 [MNHN DT-410, holotype]. A. Whole specimen. Scale: 3 cm; B. Thick section showing the thin cortex and choanosome. Scale: 1 mm; *Pachastrella ovisternata* von Lendenfeld, 1907 [MNHN DCL-4065]; C. Specimen. Scale: 3 cm; D. Thick section showing the thin cortex and choanosome. Scale: 1 mm; *Pachastrella abyssi* Schmidt, 1870 [MZS P0195, holotype]; E. Whole specimen (dry). Scale: 4 cm; F. Thick section showing the thin cortex and choanosome. Scale: 1 mm.

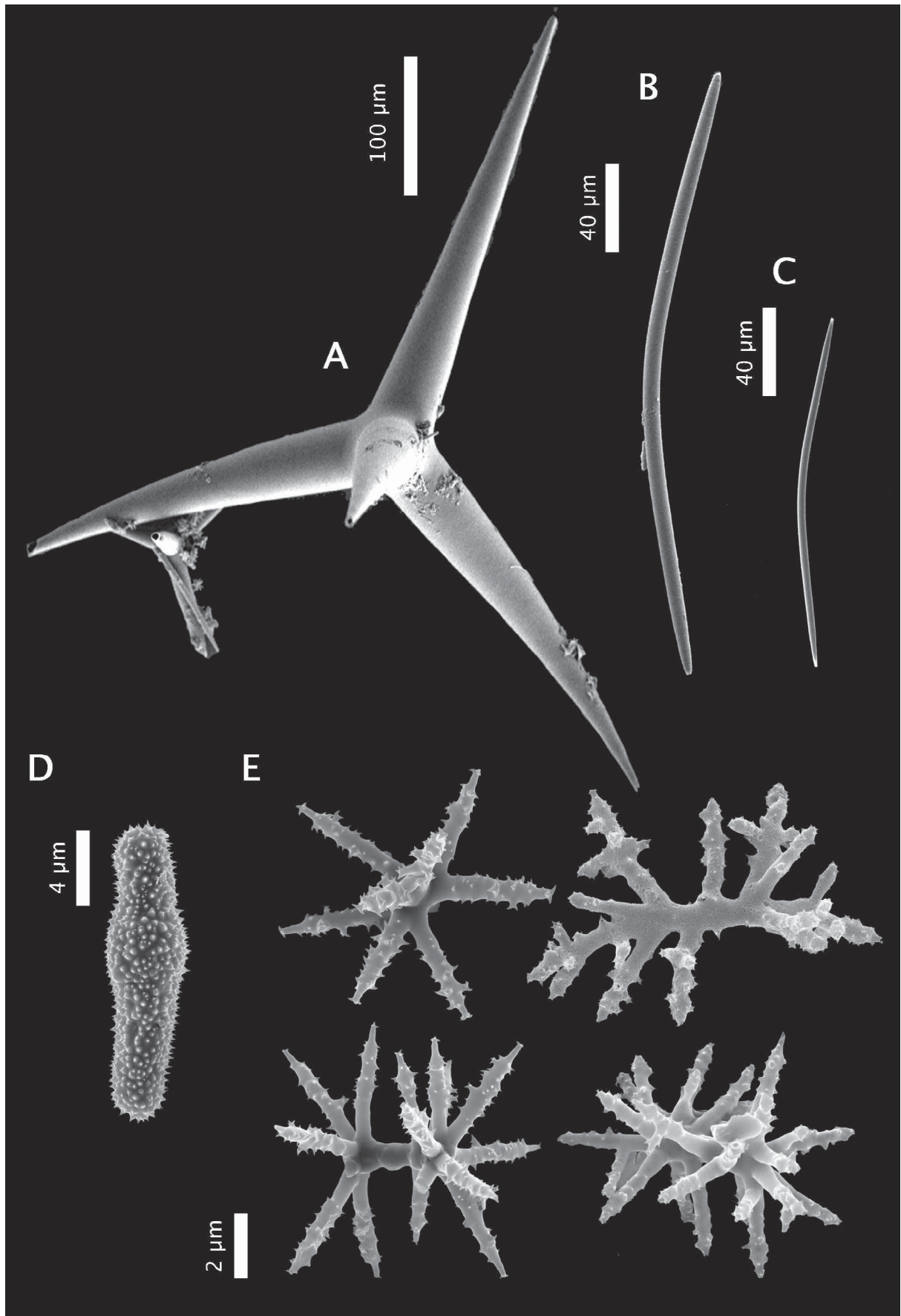


FIGURE 8. Spicules of *Pachastrella monilifera* Schmidt, 1868 [MNHN DT-756, holotype]. A. Large and small calthrops; B. Microxea I; C. Microxea II; D. microstrongyle; E. Amphiasters.

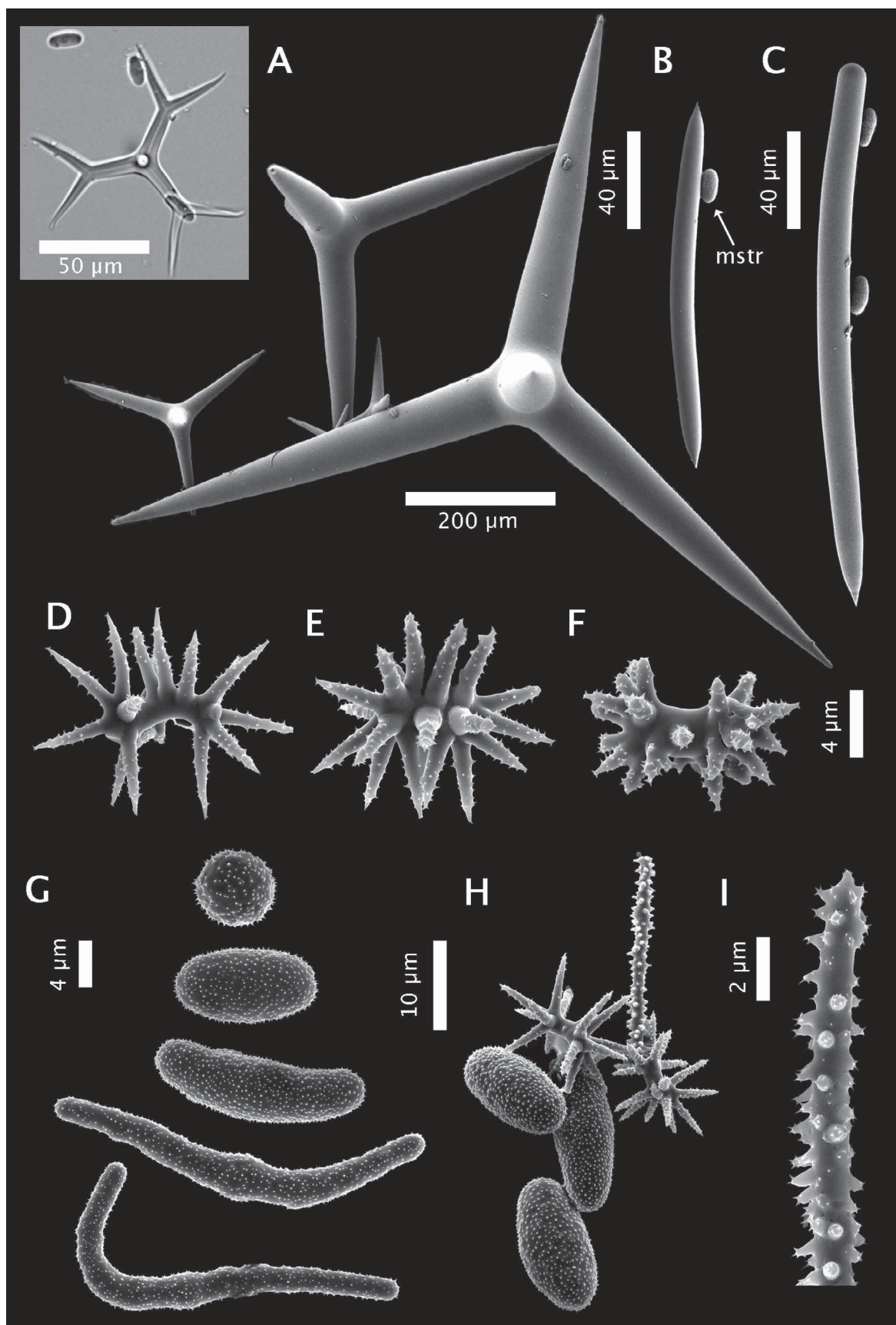


FIGURE 9. Spicules of *Pachastrella abyssi* Schmidt, 1870 [MZS P0195, holotype]. A. Large and small calthrops; B. Microxea. mstr: microstrongyles; C. Microstyle and microstrongyles; D. Amphiaster; E. Amphiaster; F. Sanidaster-like amphiaster; G. Microstrongyles; H. Microstrongyles, amphiasters and a microrhabdose streptaster; I. Detail of a microrhabdose streptaster.

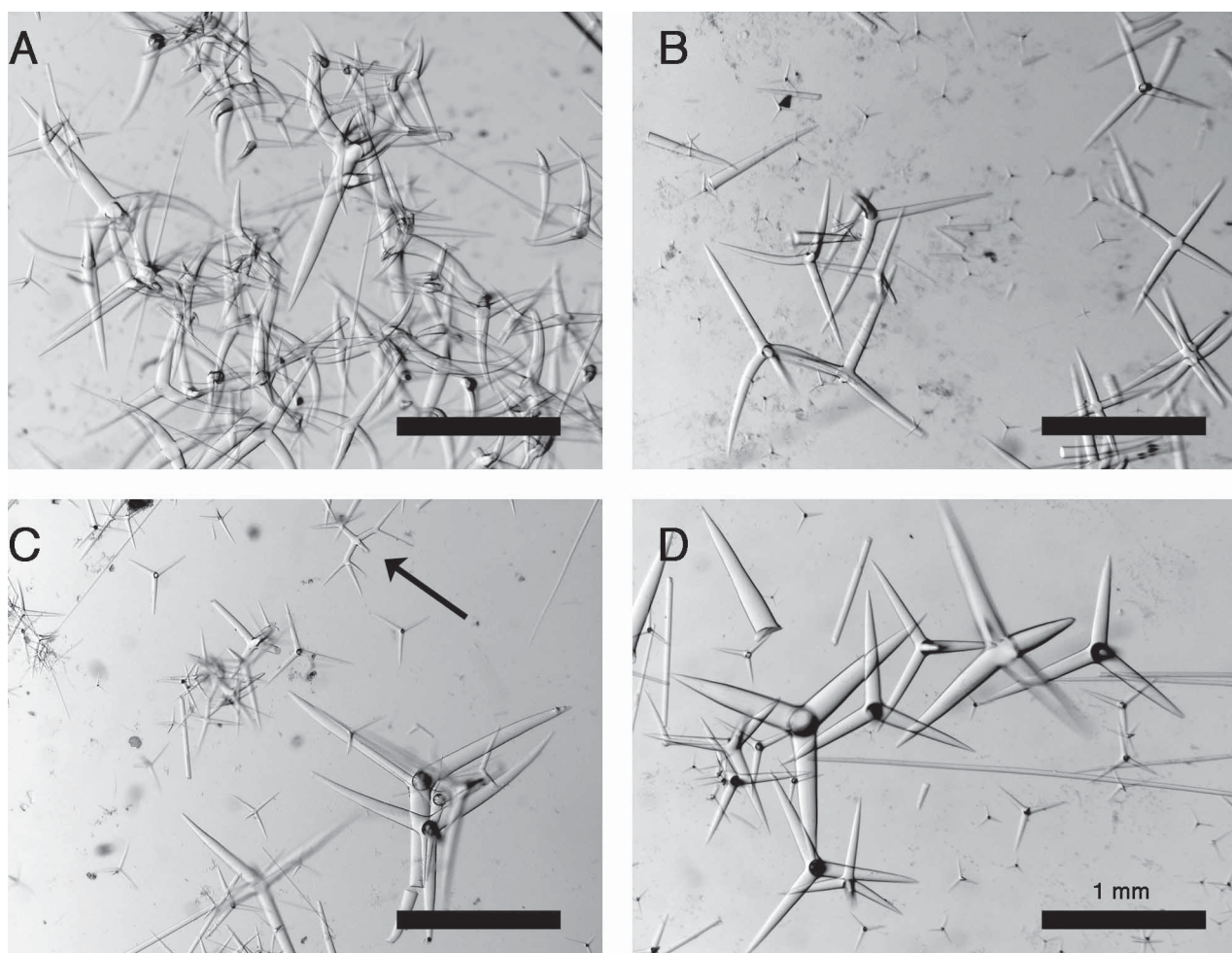


FIGURE 10. Comparison of the morphology of large calthrops. All pictures were taken at the same scale: 1 mm. A. *Pachastrella monilifera* Schmidt, 1868 [MNHN DT-756, holotype]; B. *Pachastrella nodulosa* sp. nov. [ZMBN 85242, holotype]; C. *Pachastrella ovisternata* von Lendenfeld, 1894 [MNHN DCL-4065], arrow points at a dichotriaene; D. *Pachastrella abyssi* Schmidt, 1870 [MZS P0195, holotype].

Etymology. From the latin word ‘*nodulosa*’ meaning small knot or small nodule. It refers to the knobby surface of this species.

Family Vulcanellidae Cárdenas *et al.*, 2011

Diagnosis: Astrophorida with calthrops, short-shafted triaenes or long-shafted triaenes. Aster microscleres include several categories of streptasters (spirasters, metasters, amphiasters and plesiasters). Monaxonic spicules consist of one to three categories of spiny microxeas (Cárdenas *et al.* 2011).

Genera: *Poecillastra*, *Vulcanella*.

Genus *Poecillastra* Sollas, 1888

Diagnosis: Vulcanellidae with spiny microxeas in a single category, triaenes are pseudocalthrops and/or short-shafted triaenes (Cárdenas *et al.* 2011).

***Poecillastra compressa* (Bowerbank, 1866)**

(Figure 11–13, Table 4)

Synonymy.

Ecionemia compressa Bowerbank, 1866: Bowerbank 1866, p. 55; Bowerbank 1874, p. 19.

Pachastrella compressa: von Lendenfeld 1903 p. 76; Babiç 1922, p. 284; Russ & Rützler 1959, p. 759; Sarà 1964, p. 304; Lévi 1967, p. 244.

Poecillastra compressa: Sollas, 1888 p. 98; Topsent 1890a, p. 203; Topsent 1894, p. 384; Topsent 1904, p. 89; Ferrer-Hernández 1912, p. 586; Topsent 1913a, p. 12; Stephens 1915, p. 14; Topsent 1928, p. 131; Burton 1930, p. 487; Burton 1931, p. 2; Burton 1932, p. 263; Lévi & Vacelet 1958, p. 229; Burton 1959b, p. 8; Burdon-Jones & Tambs-Lyche 1960, p. 6; Vacelet 1961, p. 23; Vacelet 1969, p. 167; Uriz 1981, p. 45; Pulitzer-Finali 1983, p. 471; Pansini 1987a, p. 157; Pansini 1987b, p. 43; Pansini & Musso 1991, Table 2; Maldonado 1992, p. 1133; Boury-Esnault *et al.* 1994, p. 47; Chombard *et al.* 1998, p. 355; Maldonado 2002, p. 154; Voultsiadou 2005, p. 57; Longo *et al.* 2005, p. 1343; van Soest *et al.* 2007, p. 129; Cárdenas *et al.* 2010, Table 1; Cárdenas *et al.* 2011, Table S1; Bo *et al.* 2012.

?*Poecillastra compressa parvistellata* Topsent, 1913b: Topsent 1913b, p. 611.

?*Poecillastra compressa antarctica* Koltun, 1964: Koltun 1964, p. 18.

Poecillastra compressa compressa Koltun, 1966: Koltun 1966, p. 32.

Poecillastra compressa (misspelling): Könnecker 1973, p. 455, Table II.

Hymeniacidon placentula Bowerbank, 1874: Bowerbank 1874, pp. 185, 189, 353.

Normania crassa Bowerbank, 1874: Bowerbank 1874, p. 258; Bowerbank 1882, p. 29.

Stelletta scabra Schmidt, 1868: Schmidt 1868, p. 19.

Poecillastra scabra: Sollas 1888, p. 99.

?*Normania crassiuscula* Sollas, 1886: Sollas 1886, p. 185.

?*Poecillastra crassiuscula*: Sollas 1888, p. 83; Topsent 1892, p. 37.

?*Poecillastra incrustans* Sollas, 1888: Sollas 1888, p. 105; Topsent 1913b, p. 610.

Poecillastra fragilis Vosmaer, 1894: Vosmaer 1894, p. 285.

Poecillastra cumana Vosmaer, 1894: Vosmaer 1894, p. 286.

Pachastrella stylifera von Lendenfeld, 1897: von Lendenfeld 1897, p. 82.

Pachastrella tenuipilosa von Lendenfeld, 1907: von Lendenfeld 1907, p. 234.

Not *Poecillastra compressa* (Bowerbank, 1866): Boury-Esnault & van Beveren 1982, p. 19 = *Poecillastra schulzei* (Sollas, 1888) (this study).

Material. ZMBN 77932, Steinneset, Langenuen, western Norway, 59°53'N, 05°3'E, 175–25 m, triangular dredge; ZMBN 87919, Sognesjøen, north of Jutevikneset, Western Norway, 61°05.8'N, 5°05'E, 240–243 m, shrimp trawl; NTNU-VM 54879, three specimens, Tømmerdalen, Trondheimsfjorden, western Norway, 63°36'46.8"N, 10°35'20.4"E, 200–250 m; ZMBN 85246, Røst Reef, northern Norway, 450 m, van Veen Grab; ZMBN 85247, Røst Reef, northern Norway, 252–299 m, manned-submersible; ZMBN 85248, Trænadjupet, northern Norway, 320 m, large box corer.

Comparative material examined.

Poecillastra compressa, ZMBN 86300, Rockall Bank, 55°26'40.6"N, 16°4'18.4"W, field # BX173-B2005, 629 m; ZMAPOR 7290, Ilhéus do Rombo, Cape Verde, 580 m; ZMAPOR 6661, off Banc d'Arguin, Mauritania, 500 m; ZMAPOR 4457, Grand Bassam, Ivory Coast; MNHN-DCL682, slide, South Africa, 37°53.3'S, 17°30'E, 309 m.

Poecillastra schulzei, MNHN-DNBE1055, slide made from holotype BMNH-1889:1:1:34, 52°04'S, 71°22'E, near Heard Island on the Kerguelen Plateau; MNHN-DNBE1280–1300, slides, originally identified as *P. compressa* (Boury-Esnault & van Beveren 1982), Kerguelen Islands, 172–315 m.

Outer morphology. ZMBN 77932 is a massive fan-shaped fragment 9 cm wide, 9 cm high and 1 cm thick (Fig. 11A). External color and choanosome of specimen alive and in ethanol was grayish. Northern Norway specimens (Fig. 11D) were white, whitish or yellowish, and either fan-shaped or massive encrusting on dead parts of the coral *Lophelia pertusa*. Specimens are compressible. Surface is regular and slightly hispid, northern Norway specimens were more hispid than the other specimens examined. There is no visible cortex. In ZMBN 77932, uniporal oscules (0.5–1.2 mm) with a conspicuous sphincter are found on the concave side of the plate and cribriporal pores on the other (each cribriporal area has a diameter of ca 2 mm). In ZMBN 85246, this arrangement is reversed: pores are on the concave side (Fig. 11D).

Skeleton (Fig. 11B). Very thin cortex (23–45 µm) that is barely visible to the naked eye: accumulation of spirasters/metasters reinforced by paratangential triaenes, oxeas and microxeas. The cortex is crossed by some oxeas I and II; they are responsible of the local hispidity. Ortho/dichotriaenes and deformed triaenes are present,

more or less positioned radially with their cladomes tangential to the cortex. There are very few triaenes in the choanosome. Apart from bundles of oxeas mainly parallel to the surface, the arrangement of the spicules in the choanosome is confused. The position of microxeas is random. Streptasters are abundant and can be found in the whole choanosome. Oxeas II are absent in the choanosome.

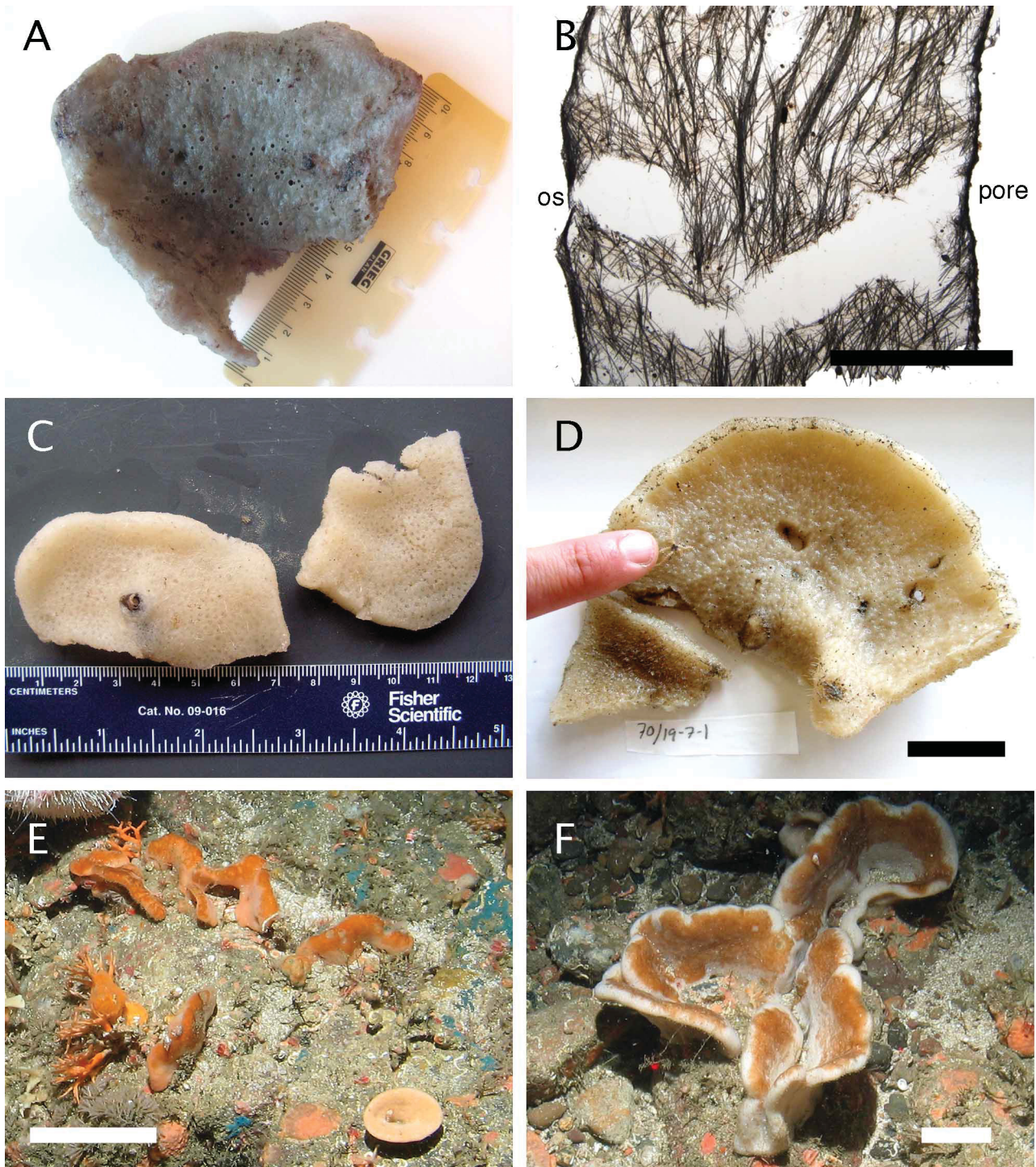


FIGURE 11. *Poecillastra compressa* (Bowerbank, 1866). A. Whole specimen from western Norway, oscule side [ZMBN 77932]; B. Thick section showing cortex and choanosome. os: oscule. Scale: 4 mm. [ZMBN 77932]; C. Whole specimens from Cape Verde, pore side [ZMAPOR 7290]; D. Whole specimen from Røst Reef, northern Norway, pore side. Scale: 3 cm [ZMBN 85246]. E. Orange specimens from Solan Bank, northern Scotland, 80 m depth (© JNCC and Annika Clements). Scale: 5 cm; F. White and orange specimen from Solan Bank, northern Scotland, 80 m depth (© JNCC and Annika Clements). Scale: 5 cm.

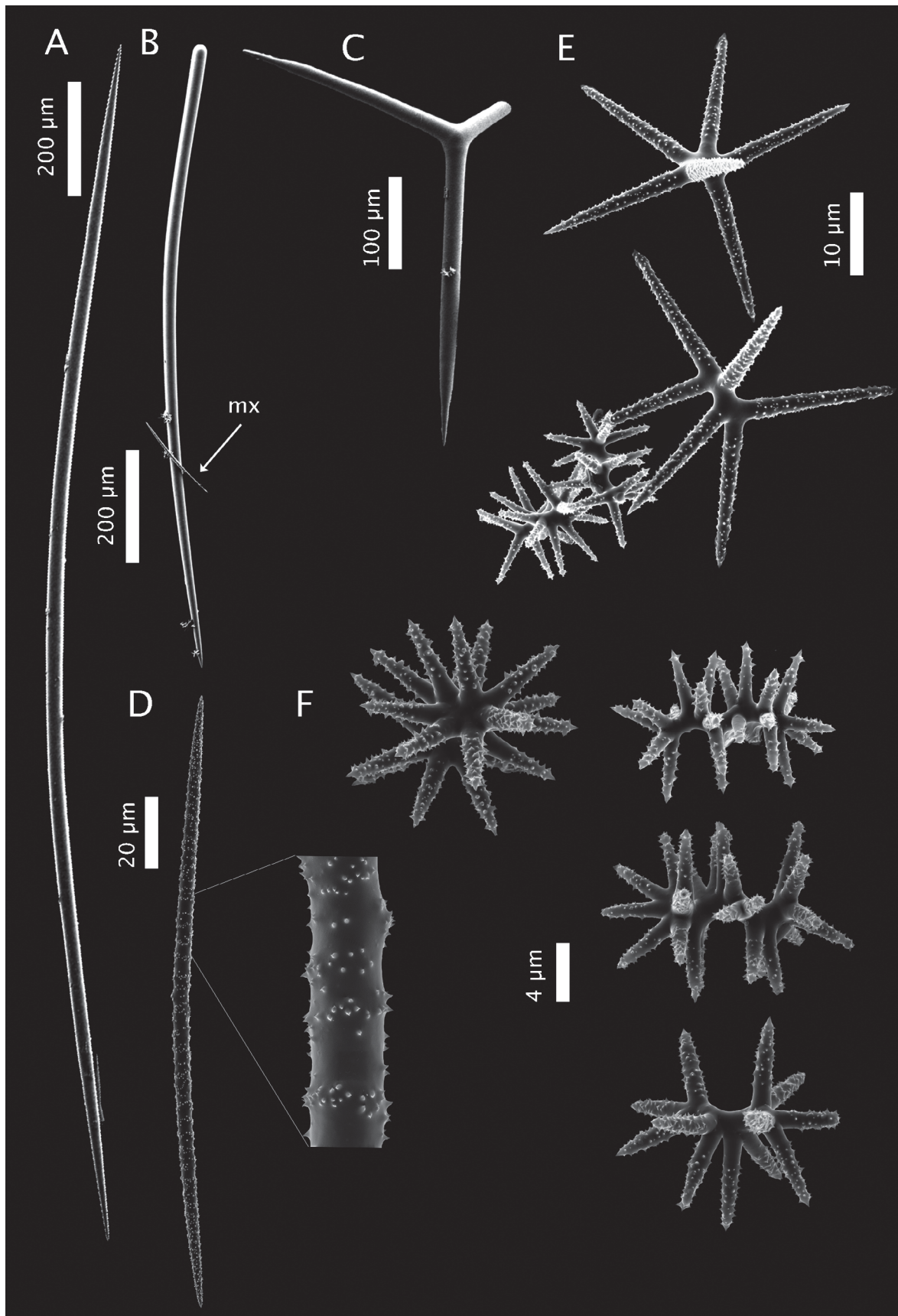


FIGURE 12. Scicules of *Poecillastra compressa* (Bowerbank, 1866) [ZMBN 77932]. A. Oxea I; B. Style. Mx: microxea; C. Short-shafted triaene; D. Microxea and detail; E. Plesiasters (with spirasters, for the lower one); F. Spiraster (upper one) to metastar (lower one).



FIGURE 13. Geographical distribution of *Poecillastra compressa* (Bowerbank, 1866).

Spicules (ZMBN 77932) (Fig. 12). (a) oxes I, stout, most are curved, sometimes modified to styles, length: 409-1068.4-2256 μm ; width: 7.0-17.4-33.0 μm . (b) oxes II, thin and pointy, bent or straight, length: more than 1200 μm ; width: 2.5-2.7-5.0 μm . (c) ortho- and dico- short-shafted triaenes (= pseudocalthrops), often irregular with deformities such as additional clads, rhabdome length: 223-297.3-420 μm (N=16); rhabdome width: 16.0-20.0-25.0 μm (N=16); clad length: 146.0-221.8-297.0 μm (N=16). (d) microxes, in high numbers, microspiny, straight or bent, rarely centrotyle, length: 141-184.2-211 μm ; width: 2.5-4.5-6.0 μm . (e) spiraster (most abundant) to metastar, microspiny actines, length: 11.5-16.3-23.0 μm ; width: 9.0-12.6-21.0 μm . (f) plesiaster, 4-8 actines, microspiny actines, diameter: 22.0-36.9-51.0 μm .

Distribution (Fig. 13). NEA: Iceland (Burton 1959b); Norway (Topsent 1913b; Burton 1930; 1931; Burdon-Jones & Tambs-Lyche 1960); Shetland and Hebrides Islands (Bowerbank 1866; 1874; von Lendenfeld 1907); Rockall bank (von Lendenfeld 1897); Porcupine Bank (van Soest *et al.* 2007); Ireland (Stephens 1915; Könnecker 1973); France (Topsent 1890a); Spain (Ferrer-Hernández 1912); Ibero-Moroccan Gulf (Boury-Esnault *et al.* 1994); Azores Islands (Topsent 1904; Topsent 1928; Lévi & Vacelet 1958); Canary Islands (Topsent 1928); Cape verde (Sollas 1888, as *P. crassiuscula*); Mauritania and Ivory Coast (this study).

Mediterranean Sea: Spain (Topsent 1894; Uriz 1981); Alboran Islands (Pansini 1987a; Maldonado 1992); France (Vacelet 1969); Corsica (Vacelet 1961); Italy (Russ & Rützler 1959; Sarà 1964; Pulitzer-Finali 1983; Pansini & Musso 1991; Longo *et al.* 2005); Adriatic Sea (Babić 1922; Pansini 1987b; Bo *et al.* in press); Aegean Sea (Voultsiadou 2005); Algeria (Schmidt, 1868, as *Stelletta scabra*).

South Atlantic: Gough Island (Topsent 1913b, as *P. compressa* var. *parvistella*, as *P. incrustans*), Tristan da Cunha (Sollas 1888, as *P. incrustans*; Burton 1932), South Africa (Lévi 1967).

Depth. 0 (in a cave, Gulf of Naples)–1740 m (Topsent 1928; Sarà 1964).

Discussion. Spicules of ZMBN 77932 are identical to those of the holotype, illustrated by Maldonado (2002). The occasional presence of styles in this species had already been noticed (von Lendenfeld 1897; Topsent 1928). There is however, one important difference: the presence of a second category of oxes in ZMBN 77932. These are not characteristic of the Norwegian population since we found similar ectosomal oxes II in the specimen from Mauritania (ZMAPOR 06661). According to Maldonado (2002), the main difference between *P. schulzei* from the southern Indian Ocean and *P. compressa* is a second category of oxea in *P. schulzei*: isodiametric ectosomal oxes. Since we found those in *P. compressa* from Norway, this difference does not stand anymore. However, we suggest here a new difference to discriminate both species: when we examined spicule slides of *P. schulzei* (including the holotype), we noted that microxes were often sharply bent or even toxa-like; this was never observed in *P. compressa*. Therefore, the holotype of *P. schulzei* should be carefully reexamined for such new specific characters, as well as its possible synonyms from the Indo-Pacific: *Poecillastra laminaris* (Sollas, 1886) and *Poecillastra eccentrica* Dendy & Burton, 1926 (Maldonado 2002). Oxes II are easy to overlook because they are only found at the surface, and may be easily scraped off during collection. Molecular data suggest that *Vulcanella* spp. and *P. compressa* are sister-groups (Cárdenas *et al.* 2011). We can therefore argue that these oxes II are homologous to the atrial oxes of *Vulcanella*, since they share a similar morphology and position. Indeed, these thin and long oxes are often found around the oscule area of *Poecillastra* species (e.i. on the fringe of the plate specimens); this is especially striking in young specimens which can have long fringes around a few oscules (Rockall Bank specimen), making them look like *Vulcanella gracilis* (Sollas, 1888). Following this, we can suggest that the atrial area of *Vulcanella* is homologous to the oscule side of *Poecillastra*.

The colors of the Norwegian specimens are whitish, grayish to light yellowish, but in Scotland (Fig. 11E, F) and in some parts of the Mediterranean, yellow or orange specimens are common (Topsent 1894; Uriz 1981; Bo *et al.* 2012). This does not seem to be due to light since orange specimens were found deeper than 100 m in the Mediterranean. Since white and orange *P. compressa* were observed living next to each other (J. Vacelet, pers. comm.) and that bi-colored specimens exist (Fig. 11F), they are in our opinion probably just color varieties.

P. compressa, like *P. monilifera*, has been considered to be a single cosmopolitan species. It shares similar environments (hard-bottoms, deep-sea coral reefs and fjords), same depth ranges and a similar distribution in the Eastern Atlantic, but unlike *P. monilifera*, hardly any morphological variations were observed between the Norwegian and Mediterranean/southern specimens, by us or previous authors (Table 4). Specimens of *P. compressa* from the English Channel, the Mediterranean Sea and the Azores have identical spicules and vary only slightly in the relative sizes of these (Topsent 1928). Sollas (1888) could not see any difference of specific value with *P. compressa* in a specimen from Queen Charlotte Islands (western Canada). However, one noticeable difference

TABLE 4. Depth, shape/color, and individual spicule dimensions (in μm) for specimens of *Poecillastra compressa* (and its synonyms) and *Poecillastra schulzei*. Means are in bold; other values are ranges; n=30 unless stated otherwise between parentheses. - = not referred.

Material	Depth (m)	Shape/color alive	Oxeas I (length/width) 409-1108.4-2400/ 7-17.7-33	Oxeas II (length/width) More than 1200/ 2.5-2.7-5	Actines of triaenes (length/width) 146-259.6-420/ 16-20.0-25 (16)	Microxeas (length/width) 141-184.7- 211/ 2.5-4.5-6	Plesiaster (diameter) 22-36.9-	Spiraster/metaster (length/width) 11.5-16.3-23/ 9-12.6-21
<i>Poecillastra compressa</i> ZMBN 77932 * Langenuen, Western Norway	25-175	Lamellar/ grayish	409-1108.4-2400/ 7-17.7-33	More than 1200/ 2.5-2.7-5	146-259.6-420/ 16-20.0-25 (16)	141-184.7- 211/ 2.5-4.5-6	22-36.9-	11.5-16.3-23/ 9-12.6-21
Shetland Islands, holotype (Sollas 1888)	201	Lamellar/-	1600-1900/ 3-45	-	170-320/ 25	140-200/-	52	20
Roscoff, France (Topsent 1894)	50	Lamellar/yellowish	1375/ 15-17	-	160/-	80-160/-	33	13-18/-
Gibraltar and off Morocco (Boury-Esnault <i>et al.</i> 1994)	293-1510	Lamellar/-	800-1027-1310/ 24-27-30	-	170-308.2-450/ 14-22-35	90-123-185/ 4-6-7		8-11-14/- (sp.1) 19-20-22/- (sp.2) 20-28-35/- (sp.3) 10-23/-
Cataluna, Spain (Topsent 1894)	126	Massive lamellar or cup/ white	1650/ 30	-	160/-	120/-	40	
Cataluna, Spain (Uriz 1981)	40-250	Lamellar/yellow or orange	900-1900/ 15-32	-	(very few)	60-120/ 3-6	30-42	10-23/-
Croatia, Adriatic Sea (Babić 1922)	82-87	Massive encrusting/ yellowish-gray	2125/ 25	-	103-290/ 17	81-200/-	26-42	19
<i>Poecillastra crassiuscula</i> Cape Verde, holotype (Sollas 1888)	182-234	Lamellar/-	2856/ 58	-	607-678/ 38-48 (few)	136/ 3.95	40	20/-
<i>P. compressa</i> var. <i>parvistellata</i> Gough Island (Topsent 1913b)	183	Cup/white	1800-2200/ 25-30	-	190-390/ 25	80-100<-120/ 3-3.5	16-23 (few)	10-13/ 4-6
<i>Poecillastra</i> sp. MNHN-DCL682 South Africa (Lévi 1967)	-	Lamellar/-	1100-2400/ 30-40	-	300-350/ 30-35	100-110/ 5	30-32 (few)	12-15/-
<i>Poecillastra</i> sp. North Kenya Banks (Pulitzer-Finali 1993)	210	Lamellar/-	Up to 3500/ 60	-	190-650/-	100-135/ 5.5	-	14-28/-
<i>Poecillastra schulzei</i> Heard Island, holotype (Sollas 1888)	274	Cup or lamellar/-	3570/ 71	4280/ 13	357-714/ 48-71	129/ 3.9	31.6	20/-

concerned pore morphology. We observed like Topsent (1913a) that the mesh size of the cribriporal pores is smaller in the Norwegian specimens than in the specimens from the Azores, Cape Verde or Ivory Coast (Fig. 11C–D). Additional data is needed to confirm the taxonomical relevance of this character. As for *P. monilifera*, genetic data is greatly needed to enlighten the status of this potential species complex.

Genus *Vulcanella* Sollas, 1886

Diagnosis: Vulcanellidae with spiny microxeas in one to three categories, with a more or less conspicuous ringed ornamentation; triaenes are calthrops and/or short-shafted triaenes or long-shafted triaenes (Cárdenas *et al.* 2011).

Vulcanella cf. *aberrans* (Maldonado & Uriz, 1996)

(Figures 14–16)

Synonymy.

Vulcanella (*Vulcanella*) *aberrans*: Cárdenas *et al.* 2011, Table S1.

Material. ZMBN 80959, Trænadjupet, northern Norway, 66°58.22'N, 11°7.26'E, 320 m, bottom: mud with rare pebbles, boxcore.

Comparative material examined.

Vulcanella aberrans, CEAB-POR.BIO 021B, paratype, slope of Alboran Island, 35°54'–35°52'N, 3°09'–3°05'W, 70–120 m; ZMAPOR 21193, Gulf of Cadiz, 35°39.274'N, 07°20.013'E, 1390 m, tiny fragment; ZMAPOR 21170, Gulf of Cadiz, 35°39.274'N, 07°20.013'E, 1390 m; ZMAPOR 18012, Morocco, near Tanger, 35°17'39.66"N, 6°47'16.18"W, 531 m.

Vulcanella gracilis, ZMAPOR 18025, off Morocco, 529 m.

Outer morphology (Fig. 14A). Massive sponge. Our specimen is broken up in several fragments. The largest, ficiform, attached to a small stone is 5 cm high and 4.5 cm wide. Color alive and in ethanol, of surface and choanosome, is whitish. Specimen is compressible. Surface is irregular, strongly hispid and dirty (due to trapped sediments). One damaged oscular basket was observed on top of the largest fragment (Fig. 14E). Oscule openings in the sieve are fairly large (exhalant apertures are 0.5–2 mm). Pores were not found.

Skeleton (Fig. 14B–D). Accumulation of spirasters and paratangential microxeas at the surface. This layer is ca 150 µm thick, thus invisible to the naked eye. Orthotriaenes and dichotriaenes are only present at the surface, albeit in low numbers. They are more or less positioned radially, with their cladomes beyond the surface (Fig. 14D). Oxeas I and some oxeas II also cross the surface. Oxeas I are found all over the surface of the sponge but they are longer and wider around the oscula. The arrangement of the spicules in the choanosome is confused. Spirasters are more rare as one leaves the surface, they are nonetheless present around canals. Plesiasters on the other hand, are abundant in the choanosome, as well as microxeas. The oscular basket is surrounded by atrial oxeas I (Fig. 14F). The oscular mesh is mainly a dense accumulation of paratangential microxeas I and streptasters. Under it, we still find microxeas, but in lower numbers. Foreign spicules in the choanosome are common (e.g. *Sceptrella* and *Hamacantha*).

Spicules (ZMBN 80959) (Fig. 15). (a) oxeas I, long and thin, isodiametric, length: up to 5000 µm; width: 3.0–6.3–14.5 µm. (b) oxeas II, stout, usually bent, smooth, length: 1921–2789–3473 µm; width: 21.0–43.6–70.0 µm. (c) ortho- and dichotriaenes, few, usually with deformities such as irregular or additional clads, rhabdome length: 152–892–1315 µm; rhabdome width: 23.0–37.6–62.0 µm; clad length for orthotriaenes: 183.0–392.9–566.0 µm (N=15); clad length for dichotriaenes: 70.0–99.0–129.0 µm + 72.0–135.0–194.0 µm (N=12). (d) microxea I, faintly microspiny, bent or straight, often centrotylote, length: 317–397.8–520 µm; width: 5.0–6.0–8.0 µm. (e) microxea II, faintly microspiny, bent or straight, length: 181–239.2–245 µm; width: 3.0–3.2–4.0 µm. (f) microxea III, faintly microspiny, straight or bent, length: 67.0–116.2–166.0 µm; width: 2.0–2.0–2.0 µm. (g) streptasters, all intermediates exist between spirasters, metasters, and plesiasters. Metasters and plesiasters often have a bow shaped shaft with the middle actines all on the same side, length: 14.0–25.0–39.0 µm.

Distribution. Northern Norway.

Depth. 320 m.

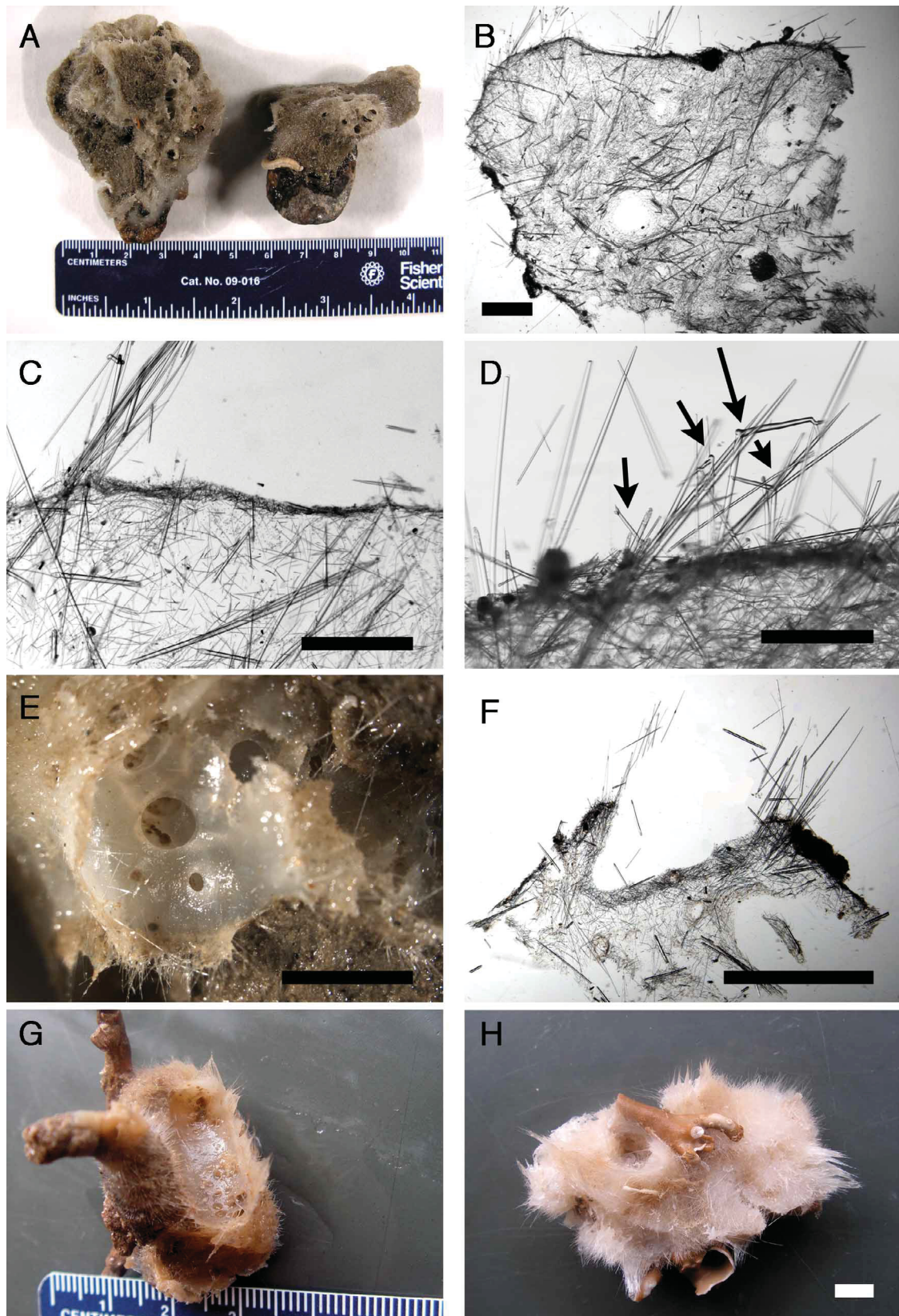


FIGURE 14. *Vulcanella* cf. *aberrans* (Maldonado & Uriz, 1996) [ZMBN 80959]. A. Whole specimens attached to small stone. The polychaete living at its base is *Eunice pennata* (Müller) (J. Kongsrud, pers. comm.); B. Thick section showing the skeletal organization. Scale: 1 mm; C. Detail of thick section showing the thin ectosome. Scale: 1 mm; D. Detail of thick section showing the irregular triaenes present at the surface (arrows). Scale: 1 mm; E. Atrial sieve. Scale: 500 μ m; F. Thick section showing the skeletal organization of the atrial sieve. Scale: 3 mm; *Vulcanella aberrans* (Maldonado & Uriz, 1996). G. Whole specimen [ZMAPOR 18012]; H. Whole specimen. Scale: 1 cm [ZMAPOR 21170].

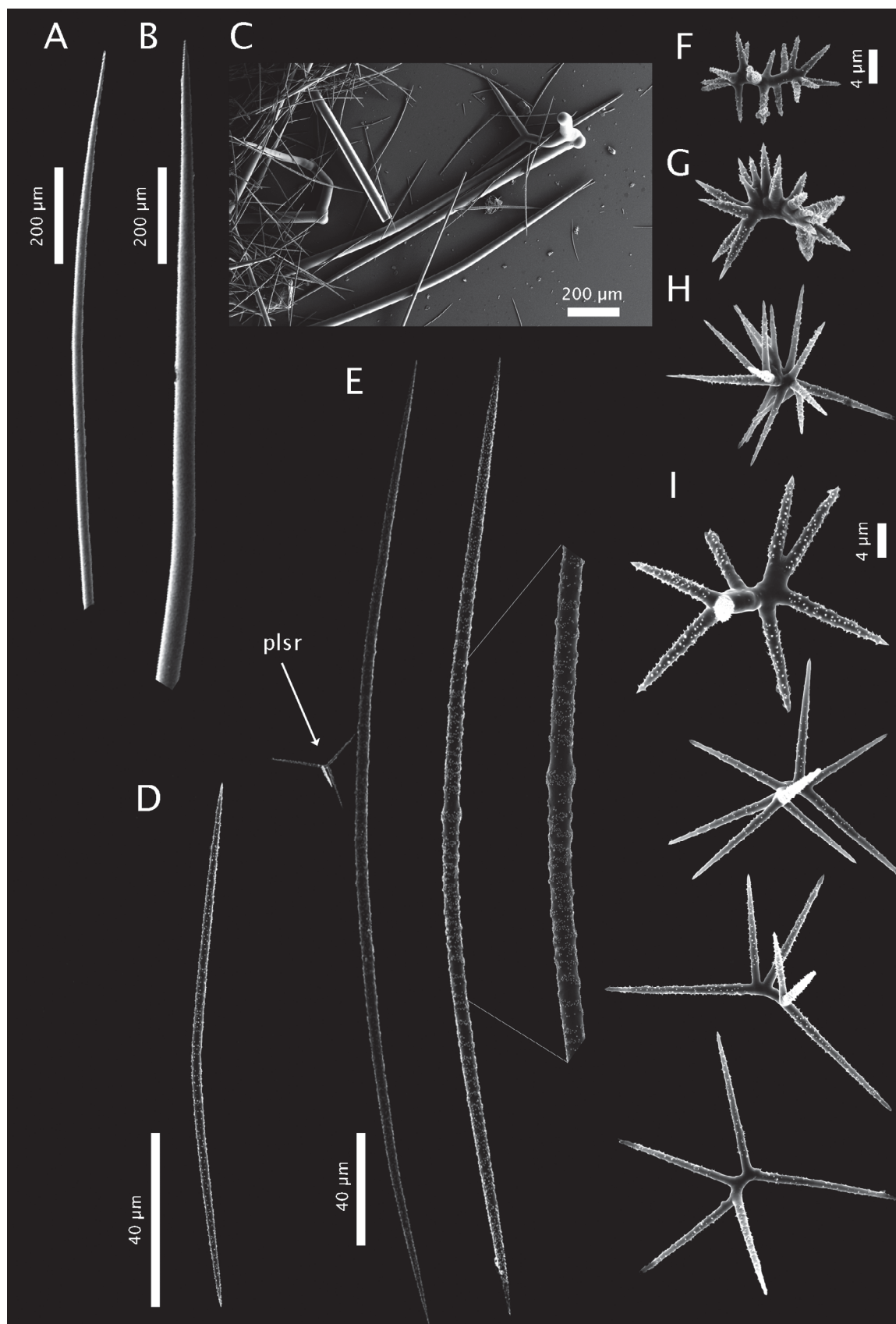


FIGURE 15. Spicules of *Vulcanella* cf. *aberrans* (Maldonado & Uriz, 1996) [ZMBN 80959]. A. Ectosomal oxea I; B. Oxea II; C. Irregular triaenes with oxea II and microxeas; D. Microxea III; E. Microxeas I, regular and centrotylote. plsr: plesiaster. Detail of the ringed pattern in the middle of the centrotylote microxea I; F. Spiraster; G. Bow-shaped metaster. Same scale as F; H. Small plesiaster. Same scale as F; I. Plesiasters. Notice the bow shape of the two lower ones.



FIGURE 16. Geographical distribution of *Vulcanella aberrans* (Maldonado & Uriz, 1996).

Discussion. If this specimen is conspecific with *V. aberrans*, this is only the second record of this species since its description, and its first record from the Norwegian coast. This specimen has been identified as *V. cf. aberrans* because it shows a few morphological and molecular differences with *V. aberrans*. Apart from (i) its shape (not plate-like) (Fig. 14A), (ii) the wider oscules in the atrial sieve (Fig. 14E), (iii) the additional category of microxea and (iv) the absence of thick-axis spirasters, the Norwegian specimen is very similar to the type material from the Alboran Island. All specimens from the Alboran Sea are plate-like (including the type and paratypes), but specimens from the Gulf of Cadiz growing on coral are more irregular in shape so the shape of our specimen could be related to the fact that it grows on yet another substrate (e.i. pebbles). The coarser atrial fenestration was also observed in ZMAPOR 18025 from the Gulf of Cadiz (Fig. 14G), so atrial fenestration should not be considered a specific character of this species. Consequently, *V. aberrans* is even more similar to the poorly known *Vulcanella cribrifera* Sollas, 1886 from Cape Verde, which is notably characterized by coarse atrial fenestration. The only differences remaining between *V. aberrans* and *V. cribrifera* are (i) rare triaene malformations, (ii) atrial strongyles and (iii) only one size category of microxeas in *V. cribrifera*. Conspecificity of *V. aberrans* with *V. cribrifera* is not impossible but more specimens of the latter are needed to settle the issue. Microxeas II and III of our specimens have very close size ranges and they might represent a single category but more specimens are needed to confirm if they are true size categories. Maldonado & Uriz (1996) observe unusually thick-axis spirasters in the atrial ectosome. Although these were observed in ZMAPOR 18012 (Morocco), these were not found in the Norwegian specimen. Altogether, this makes very few morphological characters to consider our specimen not conspecific with *V. aberrans* and we need more material from Norway to show that these differences are consistent.

COI sequences of ZMAPOR 21193 (Gulf of Cadiz) and ZMBN 80959 (Norway) are identical. Conversely, alignment of the 28S (C1-D2) sequences of the Norwegian and the Moroccan specimens showed an 8 bp. difference, most of which is due to a 6 bp. single deletion in ZMBN 80959. This is a relatively important mutation event which raises once more the question whether the few distinctive morphological differences observed are characteristic of a new species. In our opinion, additional sequences are required to conclude.

Family Theneidae Carter, 1883

Diagnosis: Astrophorida with long-shafted triaenes (sometimes lost) in combination with diverse categories of streptasters: spirasters, metasters and plesiasters (sometimes with annulate actines) (Cárdenas *et al.* 2011).

Genera: *Annullastrella*, *Cladothenea*, *Thenaea*.

Genus *Thenaea* Gray, 1867

Diagnosis: Theneidae with tetraxonic megascleres and without cladotyles.

Most of the taxonomy concerning *Thenaea* has already been treated elsewhere (Steenstrup & Tendal 1982) so our description will mainly focus on new data. Our study will notably add new records, additional illustrations (external morphology and spicules) and discuss the molecular phylogenetic data now available for those species (Cárdenas *et al.* 2011).

Thenaea abyssorum Koltun, 1964

(Figures 17, 18A–B)

Synonymy.

Thenaea muricata abyssorum Koltun, 1959 (nomen nudum): Koltun 1959, p. 662.

Thenaea abyssorum: Koltun 1964, p. 146; Koltun 1966, p. 37; Steenstrup & Tendal 1982, p. 259; Barthel & Tendal 1993, p. 83; Witte 1996, p. 571; Weslawski *et al.* 2003, p. 75; Cárdenas *et al.* 2011, Table S1.

Thenaea sp.: Babić 1915, p. 408.

Material. NTNU-VM 54948, off Vesterålen, northern Norway, 69°30.3'N, 13°55'E, 2130 m; NTNU-VM 66585, Røstbanken, northern Norway, 68°36.5'N, 11°54'E, 675–850 m.

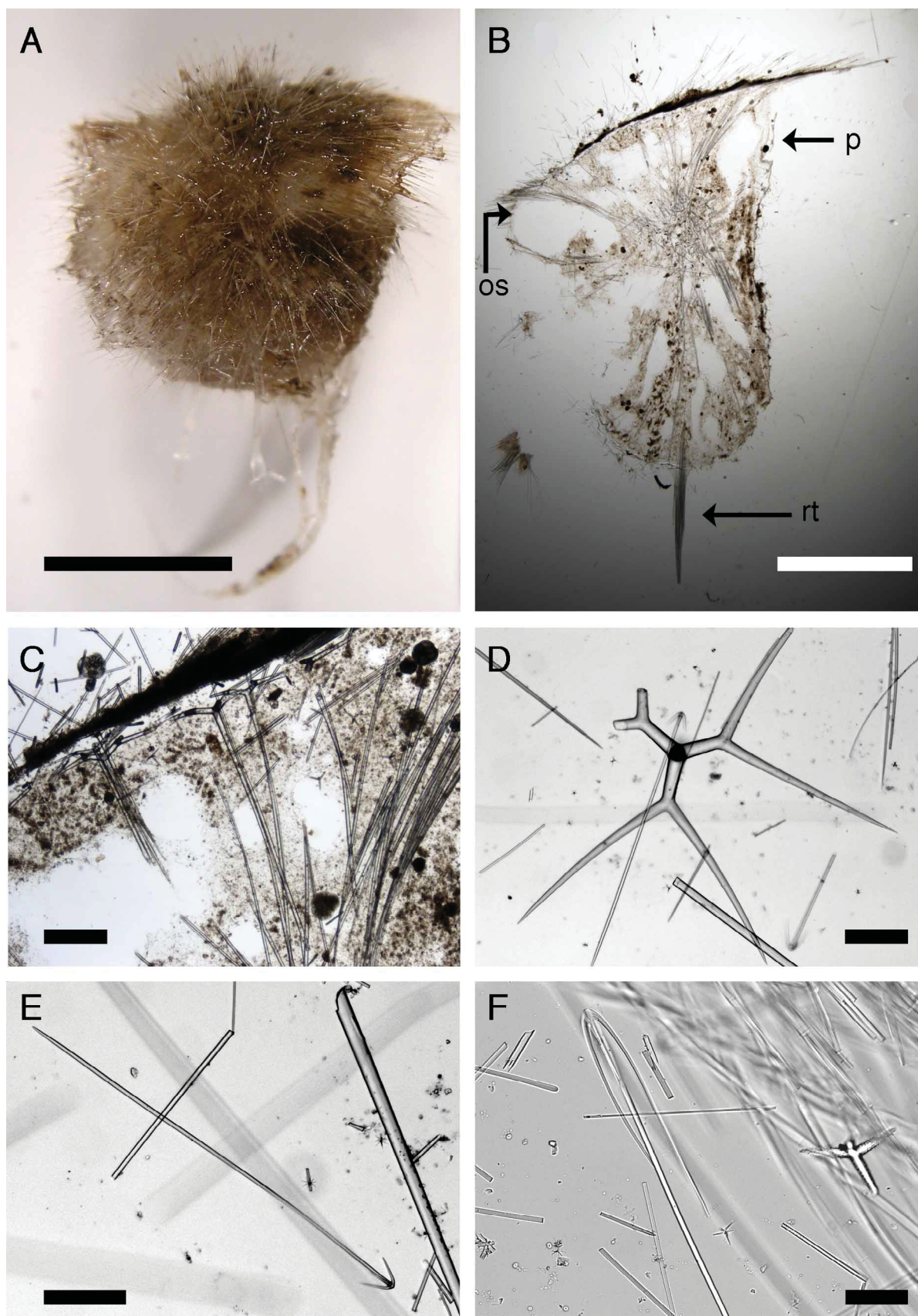


FIGURE 17. *Thenea abyssorum* Koltun, 1964 [ZMBN 85228]. A. Whole specimen. Scale: 1 cm; B. Thick section showing the skeletal organization. p: pores. os: oscule. rt: root. Scale: 5 mm; C. Thick section showing dichotriaenes supporting the ectosome. Scale: 500 µm; D. Dichotriaene. Scale: 100 µm; E. Anatriaene I. Scale: 200 µm; F. Anatriaene II, with a closed-umbrella shape. Scale: 100 µm.

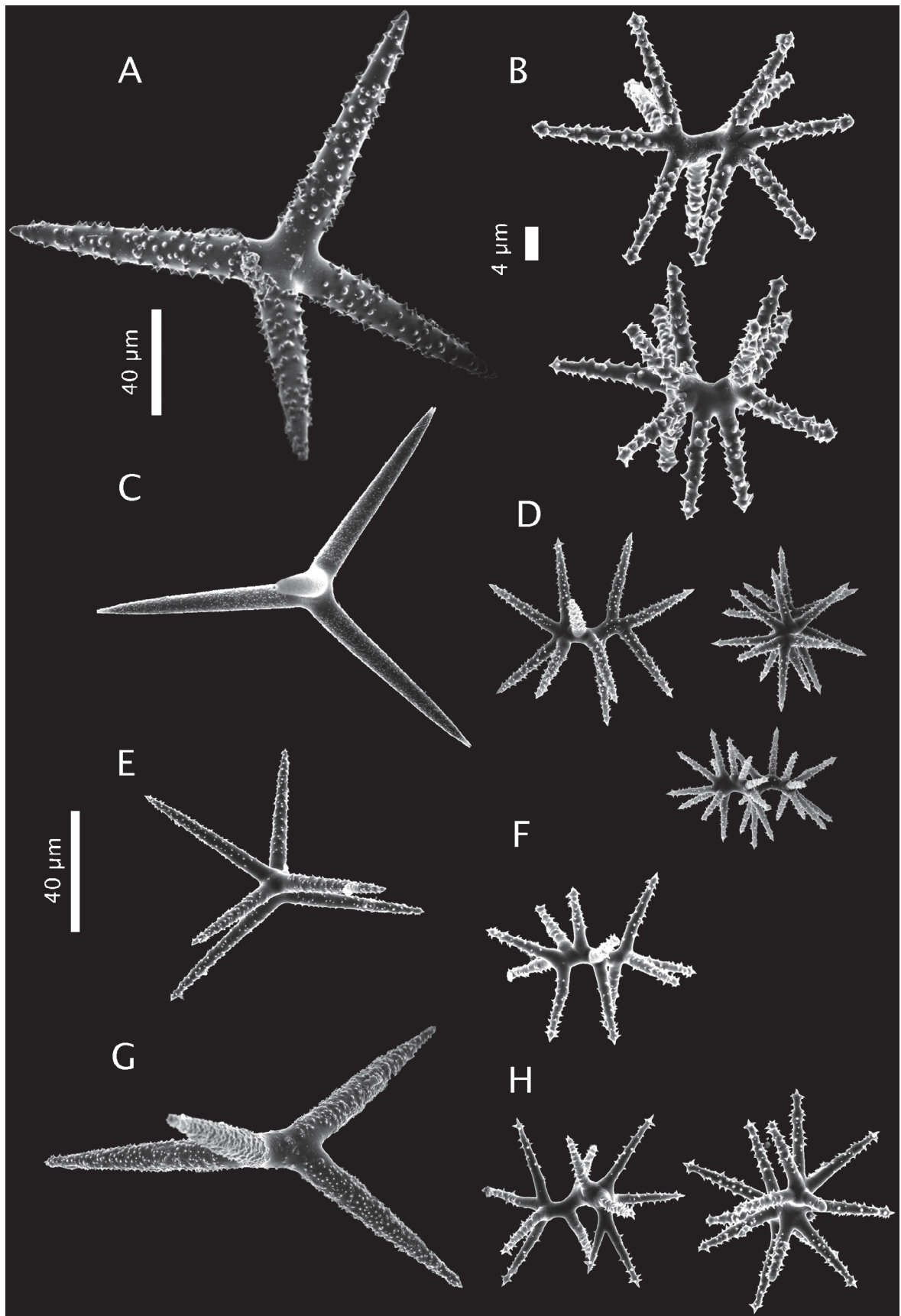


FIGURE 18. Streptasters of Norwegian species of *Thenea*. Streptasters of *Thenea abyssorum* Koltun, 1964 [ZMBN 85228]. A. Plesiaster; B. Spirasters; Streptasters of *Thenea levis* von Lendenfeld, 1907 [ZMBN 85230]. C. Plesiaster. Same scale as A; D. spirasters. Streptasters of *Thenea muricata* (Bowerbank, 1858) [ZMBN 85231]. E. Plesiaster; F. Spiraster; Streptasters of *Thenea valdiviae* von Lendenfeld, 1907. G. Plesiaster [ZMBN 85257]; H. Spirasters. Same scale as E. [ZMBN 85233].

Comparative material.

Thenia abyssorum, ZMBN 85228, Arctic mid-ocean ridge, Greenland Sea, 73°34'N, 07°45'E, H2DEEP cruise 2008, 2425–2463 m, Sneli sled (Sneli 1998).

Outer morphology (Fig. 17A). Small sub-spherical sponge (2.5 cm high, 2 cm wide) with root-like structures. Very hispid. Slightly compressible. Color alive and in ethanol is dirty brown. Choanosome is whitish to brownish (alive and in ethanol). Pores and oscule are on opposite sides (in upper part of sponge). The pore area is covered by a sieve and protected by an overhang. There is no sieve over the single oscule (ca 1 mm in diameter), it is circular and surrounded by a fringe of long oxeas.

Skeleton (Fig. 17B–C). Radial bundles of oxeas start at the center of the specimen. Many go beyond the surface, especially on the top surface, very hispid. Triaenes are found only at the surface (Fig. 17C), either crossing the ectosome or supporting it. Spirasters are abundant in the ectosome, but spirasters and plesiasters can be found throughout the choanosome (spirasters being much more common than plesiasters). The roots are made of bundles of oxeas and anatriaenes and they originate in the central part of the sponge. Anatriaenes are especially common in the basal part, always crossing the ectosome.

Spicules (ZMBN 85228) (Figs. 17C–F, 18A–B). (a) oxeas, straight, length >3750 µm; width: 20–40 µm. (b) dichotriaenes (Fig. 17C–D), rarely modified to orthotriaene or plagiotriaene, straight rhabdome or slightly bent, rhabdome length >4165 µm; rhabdome width: 20–47.2–70 µm; protoclad length: 60–132.4–210 µm; deuteroclad length: 240–480.5–850 µm. (c) anatriaenes I (Fig. 17E), common, straight rhabdome with a rather blunt tip, rhabdome length: 920–1257.5–1750 µm (N=22); rhabdome width: 5–9.0–15 µm; clad length: 45–87.8–130 µm. A more or less developed swelling can be found above the cladome. (d) anatriaenes II (Fig. 17F), common, very long and flexuous rhabdome, length between 2000 µm to more than 3600 µm; rhabdome width: 10 µm; very long clades running somewhat parallel to the rhabdome, giving to the anatriaene a closed-umbrella shape, in some cases the cladome is aborted and only an inflated tip is present, clad length: 40–279.7–548 µm (N=16). (e) prototriaenes, absent in this specimen. (f) spirasters (Fig. 18B), strongly spined, length: 25.0–36.6–57.3 µm. (g) plesiasters (Fig. 18A), 4–6 actines, strongly spined or more rarely smooth, actine length: 60–84.3–100 µm; actine width: 13–16 µm.

Reproduction. This species has been shown to be oviparous and gonochoristic, but successive hermaphroditism cannot be excluded (Witte 1996). Oogenesis takes place between June and August with spermatocysts found only in August (Witte, 1996). Subglobular buds are relatively common in this species, they are often placed at the lower half of the specimens (Barthel & Tendal 1993; Witte 1996).

Distribution. Arctic Ocean, Norwegian Sea, Greenland Sea (Steenstrup & Tendal 1982, Fig. 1D).

Depth. 850–3670 m (this study; Steenstrup & Tendal 1982).

Discussion. *T. abyssorum* is the northernmost and deepest (> 1000 m) *Thenia* species of the North Atlantic. On the field, this species can be easily confused with *T. muricata* or small *T. valdiviae*: a spicule preparation is therefore necessary. *T. abyssorum* is characterized by its large strongly spined plesiasters and streptasters. We report here for the first time a second category of anatriaene in this species, with unusually long clads (Fig. 17F).

***Thenia levis* von Lendenfeld, 1907**

(Figures 18C–D, 19, 20)

Synonymy.

Thenia levis von Lendenfeld, 1907: von Lendenfeld 1907, p. 215; Steenstrup & Tendal 1982, p. 259; Klitgaard 1995, p. 1; Cárdenas *et al.* 2011, Table S1.

Material. ZMBN 85230, 85249, West of Marstein, western Norway, 60°8'18"N, 4°50'47"E, 300 m, Agassiz trawl; NTNU-VM 55838, 55839, 55842, Haltenbanken, western Norway, 64°14'56"N, 9°0'3.7"E; ZMBN 85250, Røst reef, northern Norway, 67°30.41'N, 9°25.60'E, 312 m, large boxcore; ZMBN 85229, Sotbakken, northern Norway, 70°45.32'N, 18°40.11'E, 286 m, large boxcore; University of Tromsø, Marbank, field# M07GOS0081-7, off Tromsø, 71°08'N, 18°39.33'E, 190 m, beamtrawl.

Comparative material.

Thenia levis, ZMAPOR 21501, SW of Rockall Bank, 55°31'7.9"N, 15°48'27.54"W, 844–857 m.

Description. *Outer morphology*. Massive elongated sponge. ZMBN 85230 is straight (8 cm long, 2 cm high) (Fig. 19A) while ZMBN 85249 (6.5 cm long, 2.5 cm high) is slightly bent. Both have a minutely hispid surface.

ZMBN 85251 (3 cm long, 2 cm high) is very hispid with very long hair-like oxeas. Specimens are not compressible. Color alive and in ethanol is brown. Choanosome is whitish to brownish (alive and in ethanol). Pore and oscule areas (both with sieves) are along the longitudinal sides, opposite to each other. They are more or less long and high. A thick overhang protects the pore area (Fig. 19B). Small roots extend from the base of the sponge.

Skeleton (Fig. 19C–D). Like *T. abyssorum* except for the presence of many protriaenes (below the ectosome) and abundance of plesiasters, especially near the poral area (Fig. 19C).

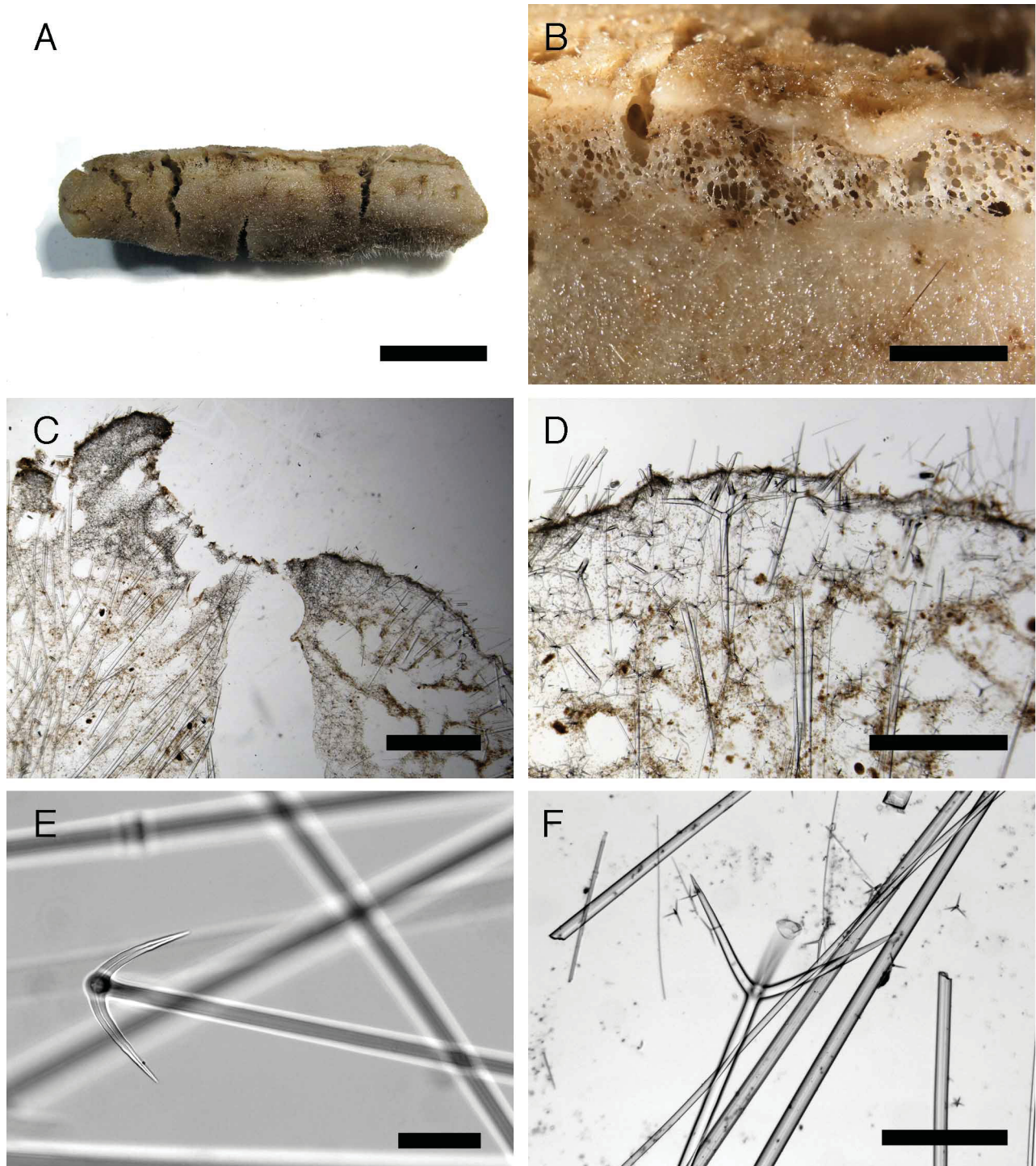


FIGURE 19. *Thenea levis* von Lendenfeld, 1907 [ZMBN 85230]. A. Whole specimen. Scale: 2 cm; B. Detail showing the cribriform pores, with a thick overhang. Scale: 4 mm; C. Thick section of sieved pores. Scale: 2 mm; D. Thick section showing skeletal organization of ectosome. Scale: 1 mm; E. Anatriaene. Scale: 100 μ m; F. Protriaene. Scale: 500 μ m.

Spicules (ZMBN 85230) (Figs. 18C–D, 19D–F). (a) oxeas, stout, straight or slightly bent, length: 3375–5311.5–7750 μm (N=13); width: 35–70–95 μm (N=17). (b) dichotriaenes (Fig. 19D), straight rhabdome, length: 4500–5187–6500 μm (N=4); width: 33–58.6–85 μm ; protoclad length: 130–196.3–260 μm ; deuteroclid length: 230–574.8–950 μm . (c) anatriaenes (Fig. 19E), straight rhabdome (which can become flexible at its end), many irregular swellings were observed on some rhabdomes, length up to 1,35 cm; rhabdome width: 5–14.4–20 μm ; clad length: 15–111.9–160 μm (N=14). A more or less developed swelling can be found above the cladome. (d) prototriaenes (Fig. 19F), common, straight, rhabdome length: from 3825 μm to >5700 μm ; rhabdome width: 40–54.1–75 μm (N=18); clad length: 400–609.6–1200 μm (N=14). (e) spirasters (Fig. 18D), spined, length: 17,5–21,4–29,1 μm . (f) plesiasters (Fig. 18C), very abundant, 3–6 actines, faintly spined (not visible with an optical microscope), actine length: 30–83,7–145 μm ; actine width: 4,2–10,8–24,3 μm .

Distribution (Fig. 20). South-East Greenland, Denmark Strait and Iceland (Steenstrup and Tendal, 1982); Norway and western Barents Sea (Tendal *et al.* 2001; this study); north of Wyville Thomson Ridge (von Lendenfeld, 1907); Rockall Bank (this study).

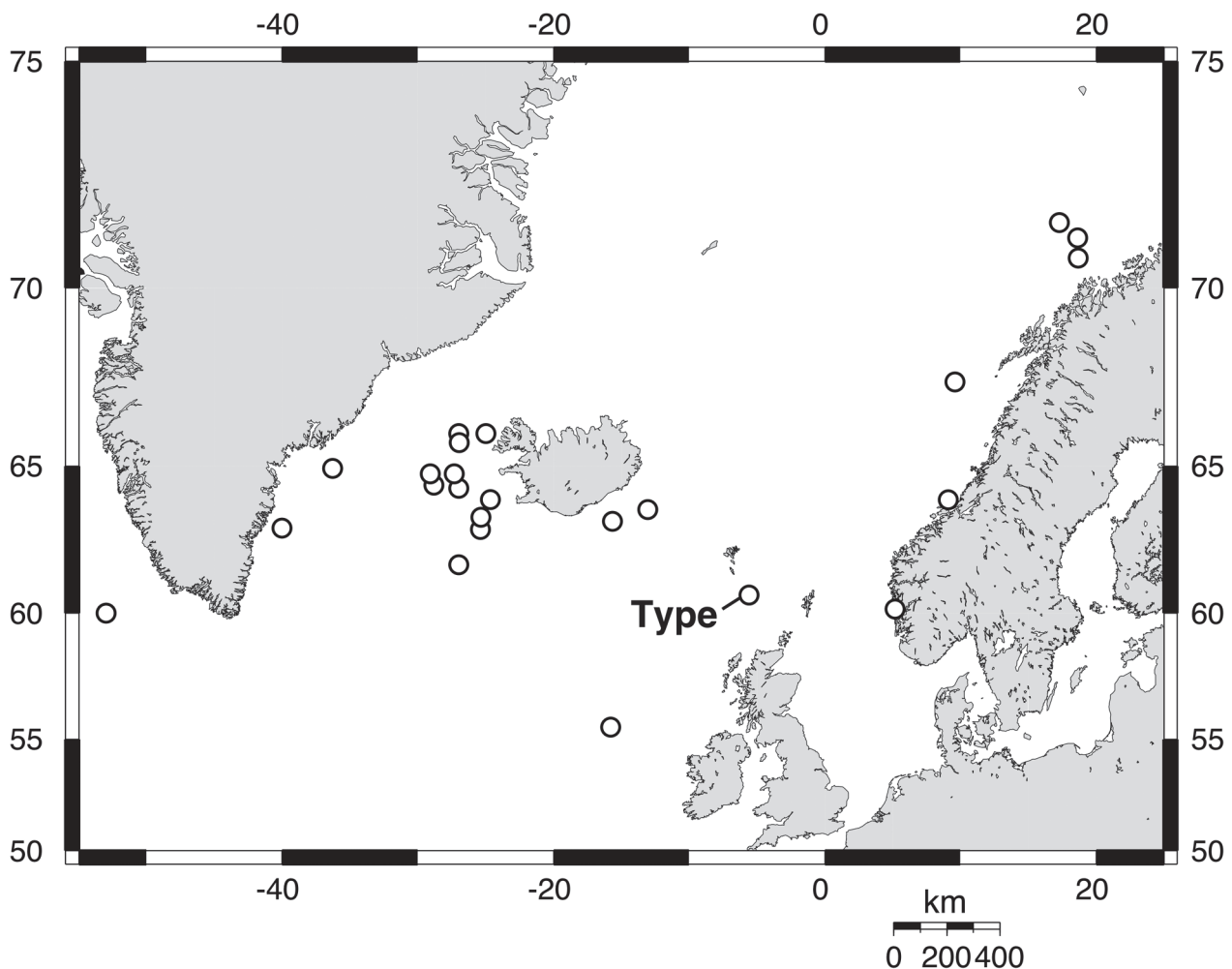


FIGURE 20. Geographical distribution of *Thenea levis* von Lendenfeld, 1907. Localities from Steenstrup and Tendal (1982) and those from this study.

Depth. 190–1480 m (this study; Steenstrup & Tendal 1982).

Discussion. This is the first record of *T. levis* from Rockall Bank. These findings extend its geographical range to the south (Fig. 20). It is sympatric with *T. muricata* in the Greenland/Iceland/southern Norway area, and sympatric with *T. valdiviae* in northern Norway. The spicules measured in our specimen (ZMBN 85230) fit the general redescription given by Steenstrup and Tendal (1982) except for the presence of mesoprotriaenes and prodiaenes that we did not find. The plesiasters of *T. levis* are on average as large as in *T. abyssorum* but there is a wider range of sizes and they are not strongly spined. The spirasters of *T. levis* are smaller than in *T. abyssorum* and

in the same size range as in *T. muricata* and *T. valdiviae*. SEM pictures (Fig. 18) suggest that *T. levis* plesiasters are more delicately spined than *T. muricata* and *T. valdiviae* plesiasters: the spines are not only smaller but their density is higher, more uniform (same goes for the spirasters). However, to generalize this observation, one would need to look at many more specimens with the SEM. The distinctive elongated shape with longitudinal opposite poral and oscular areas may be used to identify *T. levis* in the field.

***Thenaea muricata* (Bowerbank, 1858)**

(Figures 18E–F, 21–23, Table 5)

Synonymy (modified from Maldonado (2002)).

Tethea muricata Bowerbank, 1858: Bowerbank 1858, p. 308, pl. 25. fig. 18; Bowerbank 1872, p. 115, pl. V, figs. 1–6.

Thenaea muricata: Gray 1867, p. 541; Sollas 1888, p. 95; Topsent 1892, p. 37; Topsent 1894, p. 375; Lambe 1896, p. 202; Lambe 1900, p. 26; Topsent 1913a; Stephens 1915, p. 11; Ferrer-Hernández 1922, p. 2; Sarà 1958, p. 216; Gamulin-Brida 1969, p. 89; Pulitzer-Finali 1972, p. 348; Uriz 1981, p. 48; Steenstrup & Tendal 1982, p. 259; Pulitzer-Finali 1983, p. 474; Pansini 1987b, p. 43; Uriz & Rosell 1990, p. 48; Pansini & Musso 1991, Table 2; Boury-Esnault *et al.* 1994, p. 51; Maldonado 2002, p. 156; Voultsiadou 2005, Table 1; van Soest *et al.* 2007, Table 2; Cárdenas *et al.* 2011, Table S1.

Ancorina (Thenaea) muricata: von Lendenfeld 1903, p. 53.

?*Ancorina (Thenaea) muricata*: Babiç 1914, p. 152.

Wývillethomsonia wallichii Wright, 1870: Wright 1870, p. 8.

Thenaea wallichii: Sollas 1882, p. 427.

Dorvillia agariciformis Kent, 1870: Kent 1870, p. 293.

Tisiphonia agariciformis: Thomson 1873, p. 167.

Clavellomorpha minima Hansen, 1885: Hansen 1885, p. 19.

?*Thenaea (muricata) schmidtii* Sollas, 1886: Babiç 1915, p. 389; Babiç 1922, p. 282.

Thenaea intermedia Sollas, 1888: Sollas 1888, p. 97.

Not *Thenaea schmidtii* Sollas, 1886: Sollas 1886, p. 183; Sollas 1888, p. 67 (this study)

Material. ZMBN 85232, Brattholmen, Hjeltefjord, western Norway, 100 m; ZMBN 85252(a/b), Bømlafjorden, Midtvikøy, western Norway, 59°40'N, 5°24'E, 230–90 m, triangular dredge; ZMBN 85231, west of Marstein, western Norway, 60°8'18"N, 4°50'47"E, 300 m, Agassiz trawl; ZMBN 87920, Sognefjorden deep basin, off Lånefjorden, Western Norway, 61°08.3'N, 6°10'E, 1232–1225 m, Agassiz trawl; ZMBN 85253, mid Norway, 63°08.54'N, 8°13.37'E, 165 m, Møre 2006 cruise; NTNU-VM 54908, Trollsteinen, mid Norway, 64°35'59.9"N, 11°1'30"E, 420 m; NTNU-VM 54909, Kinebbneset, Trondheimsfjorden western Norway, 63°32'28"N, 9°49'47.2"E; NTNU-VM 55655, Tautra, Trondheimsfjorden, mid Norway, 63°32'17.99"N, 10°30'33.99"E, 160 m; NTNU-VM 55622, north of Smøla Island, mid Norway, 63°37'50"N, 7°59'14.9"E, 300 m; NTNU-VM 55843, Haltenbanken, mid Norway, 64°14'56"N, 9°0'3.7"E.

Comparative material.

Thenaea muricata, ZMAPOR 19481, Rockall Bank, 55°31'7.9"N, 15°48'27.54"W, 844–857 m; MNHN-DCL3436, Banuyls, France, 800 m, Ecomarge 1985; MNHN-DCL4083, off Cape Santa Maria di Leuca, Italy, 39°34.01'N, 18°26.16'E, 585 m, MEDECO 2007 cruise; ZMBN 85254, Gulf of Cadiz, Balgim campaign, St. CP25, 36°41'5"N, 7°19'4"W, 544 m.

Thenaea schmidtii, ZMAPOR 18036, Gulf of Cadiz, 35°47'59.9"N, 7°47'59.9"W, 443 m.

Outer morphology (Fig. 21A–B). Massive sub-spherical sponge. ZMBN 85231 is 2.8 cm long and 2.6 cm high. ZMBN 85252(a/b) are made of “fused specimens” (4–8 cm of diameter). These larger specimens have many string-like buds on its top surface, these can reach 2 cm long. ZMBN 85232 is a half damaged specimen. All specimens are slightly compressible. Surface is minutely hispid, like sand-paper. Color alive and in ethanol is brown. Choanosome is whitish to brownish (alive and in ethanol). Single, circular to ellipsoid oscule situated in the top (3 mm in ZMBN 85231, 1–4 mm in ZMBN 85252); a conspicuous whitish sphincter surrounds it and there is no sieve. The sieved pore area runs along the equatorial side of the specimen (ZMBN 85231) or can extend itself in the entire lower part of the specimen (ZMBN 85252). All specimens have roots.

Skeleton (Fig. 21C–D). Like *T. abyssorum*. Depending on where the section is made, plesiasters are rare (especially in the choanosome) to very abundant (especially under the ectosome). Protriaenes are found under the ectosome as well (Fig. 21D), they can be rare to common depending on the specimen. Anatriaenes were observed in the choanosome associated in bundles with triaenes (Fig. 21D); they were also observed coming out of the top surface.

Spicules (ZMBN 85231) (Figs. 18E-F, 21D-F). (a) oxeas, slightly bent, length: 4000-5196.4-5925 μm (N=7); width: 30-41.4-55 μm (N=7). (b) dichotriaenes (Fig. 21D-E), rhabdome is straight to bent, or even flexuous, length: 1925-2972-3875 μm (N=9); width: 23-49.6-80 μm ; protoclad length: 190-284.5-370 μm ; deutero-clad length: 350-564-900 μm . (c) anatriaenes (Fig. 21F), common, straight, bent or flexuous rhabdome, length: 1550-3976.1-4675 μm (N=23); rhabdome width: 5-11.8-22 μm ; two shapes, the smaller ones, probably younger forms (with clad length: 60-85 μm and rhabdome width: 5-9 μm) have a regular umbrella-shape, the larger more common ones have bent clads, clad length: 60-157.1-242 μm . (d) prototriaenes, rare, straight, rhabdome length >1000 μm ; rhabdome width: 50 μm (N=1); clad length: >600 μm (N=1). (e) spirasters (and few metastars) (Fig. 18F), spined, length: 13-23.2-32.5 μm . (f) plesiasters (Fig. 18E), 3-7 actines, faintly spined (hardly visible with an optical microscope), actine length: 16.6-37.0-70.3 μm ; actine width: 1.7-3.5-10 μm .

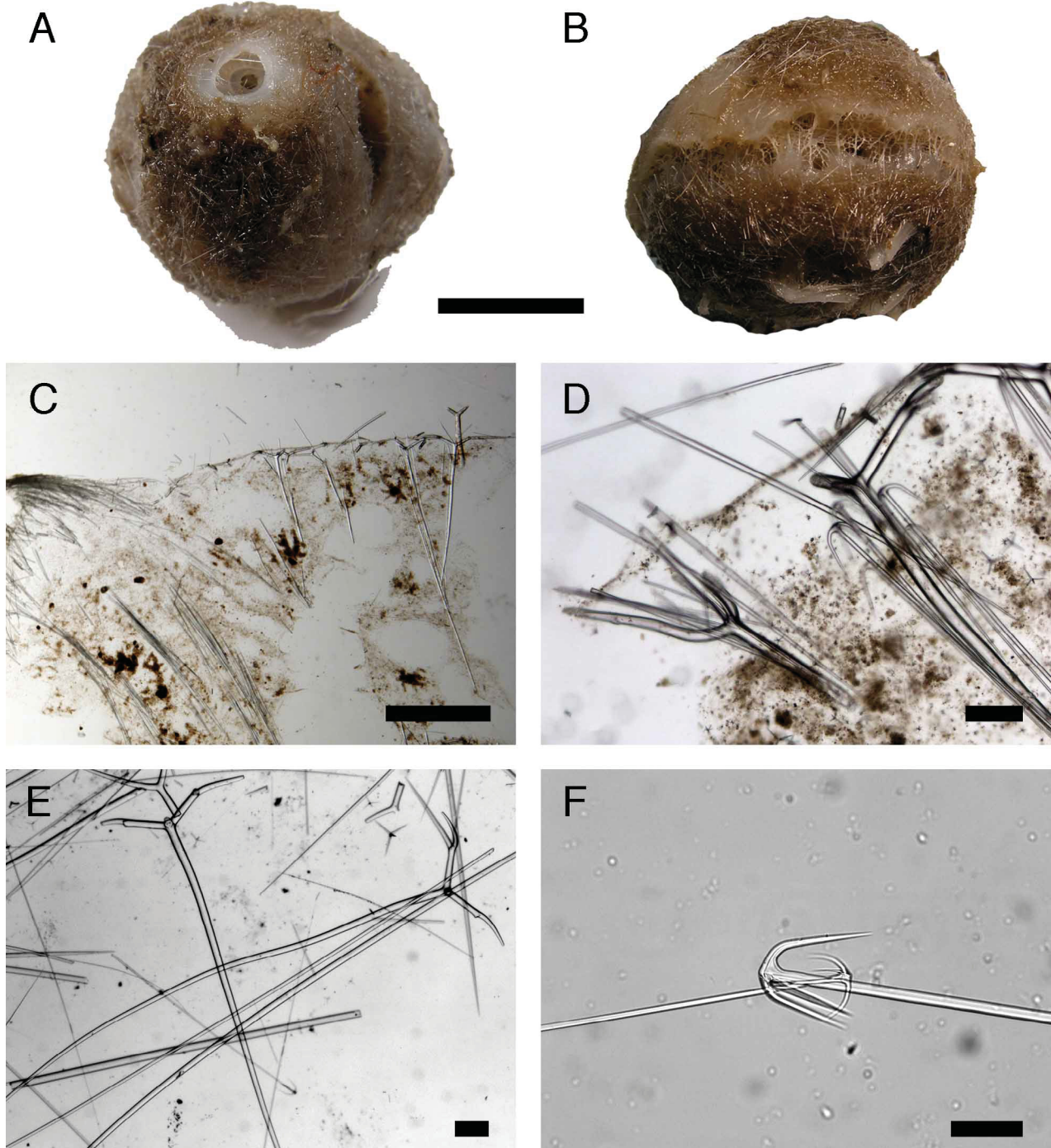


FIGURE 21. *Thenea muricata* (Bowerbank, 1858) [ZMBN 85231]. A. Whole specimen, upper view showing oscule. Scale: 1 cm; B. Whole specimen, side view showing the pore area. Same scale as A; C. Thick section of ectosome and choanosome. Scale: 2 mm; D. Close-up of thick section showing dichotriaene, anatriaenes and a prototriaene placed under the ectosome. Scale: 200 μm ; E. Dichotriaenes. Notice the flexuous rhabdome. Scale: 200 μm ; F. Anatriaenes, large and small size. Scale: 200 μm .

Reproduction. We observed oocytes in vitellogenic phase (A. Ereskovsky, pers. comm.) in the thick sections of *T. schmidtii* (ZMAPOR 18036, collected at the end of August 2004) and *T. muricata* (ZMBN 85231, collected mid-June 2008). Spermatogenesis has been observed in *T. muricata* from Norway, possibly collected in May (Sollas 1882). Oocytes and spermatocytes have already been observed simultaneously in *T. muricata* from the Adriatic Sea indicating that this species can be hermaphrodite (Babiç 1915). Elongated thread-like buds are common on the upper surface of large Norwegian specimens (e.g. ZMBN 85252) whereas they seem to be more subglobular in Mediterranean samples (Uriz 1981, Fig. 28).

Distribution (Fig. 22). Greenland, Denmark Strait and southern Iceland (Steenstrup & Tendal 1982); Norway (Bowerbank 1872; Sollas 1882; Topsent 1913a; Steenstrup & Tendal 1982); Rockall Bank (van Soest *et al.* 2007); northern Spain (Ferrer-Hernández 1922); Azores (Topsent 1892; 1904); Gulf of Cadiz (Boury-Esnault *et al.* 1994); Mediterranean Sea (Sollas 1888; Sarà 1958; Gamulin-Brida 1969; Pulitzer-Finali 1972; Uriz 1981; Pulitzer-Finali 1983; Uriz & Rosell 1990; Pansini & Musso 1991; Boury-Esnault *et al.* 1994; Voultsiadou, 2005); ?Canada (Topsent 1892; Lambe 1896).

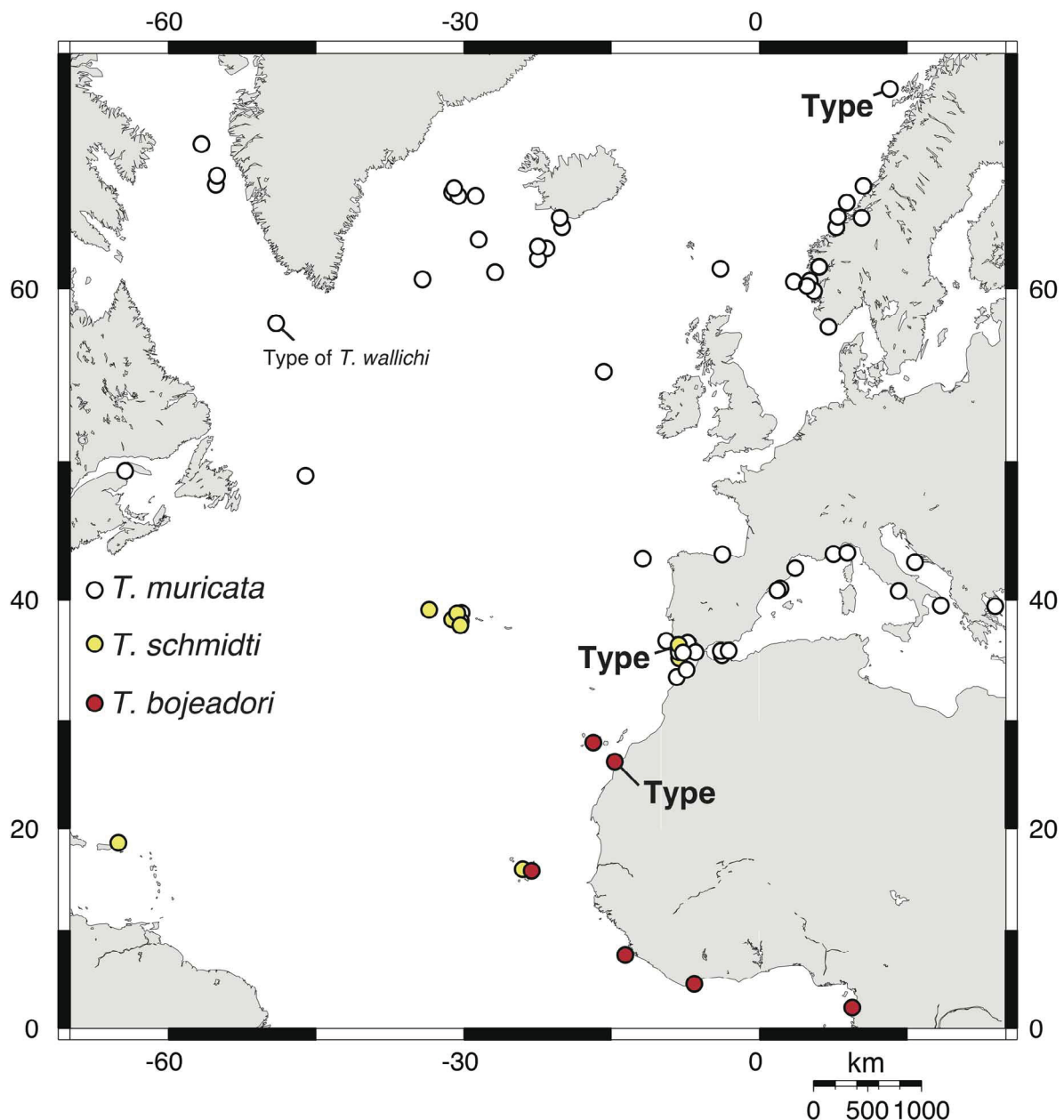


FIGURE 22. Geographical distribution of *Thenea muricata* (Bowerbank, 1858). Localities given by Hansen (1885), Fristedt (1887), Sollas (1888), Topsent (1913) and Stephens (1915) were discarded not knowing if some of these could be *T. valdiviae*.

As *T. schmidtii*: Puerto Rico (Sollas 1888); Azores (Topsent 1892;1904); Gulf of Cadiz (Sollas 1888; this study); Cape Verde (van Soest 1993); Mediterranean Sea (Babiç 1915; 1922; Pansini 1987b).

Depth. For *T. muricata*: 60-2940 m (Steenstrup & Tendal 1982; Voultsiadou 2005); for *T. schmidtii* in the Azores: 349–4020 m (Topsent 1904).

Discussion. The Norwegian specimens fully agree with the redescription of this species (Steenstrup & Tendal 1982). It is the most widespread *Thenia* species (Fig. 22): its northernmost localities are at the moment in Eastern Greenland and the Denmark Strait while its southernmost localities are off Morocco. We have never identified *T. muricata* in northern Norway or the Barents Sea. We re-examined the *T. muricata* specimens (ZMAPOR 2385) collected by Vosmaer (1885) in the Barents Sea, and re-identified them as *T. valdiviae* based on the presence of sieves covering their oscules (vs. “naked” oscules with a conspicuous whitish sphincter in *T. muricata*). We therefore agree with Steenstrup and Tendal (1982) that other arctic records of *T. muricata* are likely to be *T. valdiviae* (e.g. Hansen 1885; Koltun 1966). *T. muricata* from the Zanzibar area is suspicious and probably a misidentification (Burton 1959a).

T. schmidtii is distributed from the Azores to Gibraltar (Fig. 22) and originally characterized by i) a high-density of larger plesiasters, ii) a poorly developed choanosome tissue, iii) larger choanocyte chambers and iv) a large oscule sphincter (Sollas, 1888). Our specimen of *T. schmidtii* (Fig. 23) corresponds in every point to this description. Stephens (1915) compared her Irish *T. muricata* with *T. schmidtii* and often could not tell which one had the most plesiasters. Indeed, Norwegian *T. muricata* could show abundant plesiasters but these were localized in certain areas (e.g. under the ectosome), whereas *T. schmidtii* appeared uniformly filled with plesiasters (Fig. 23C–D).

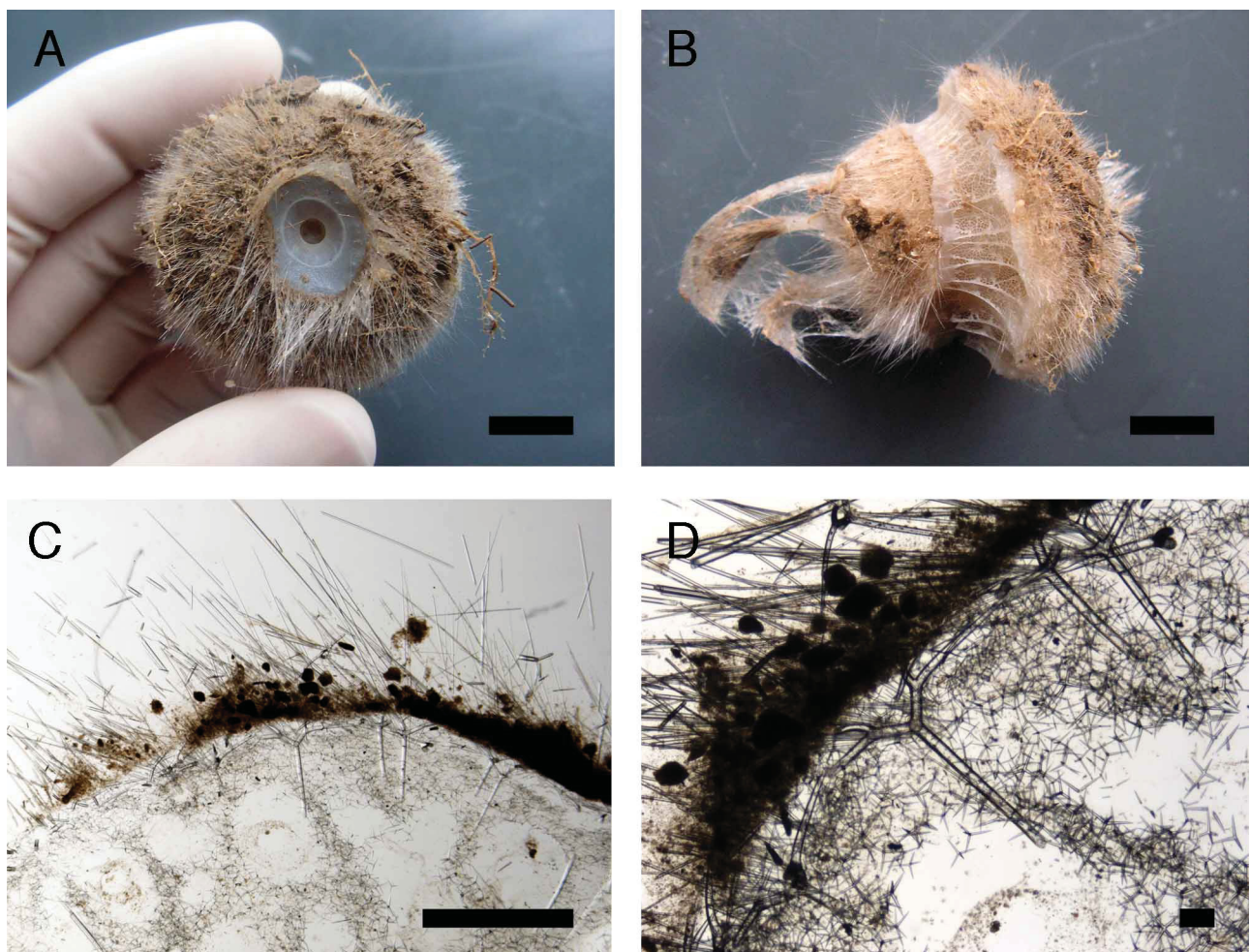


FIGURE 23. *Thenia schmidtii* Sollas, 1886 [ZMAPOR 18036]. A. Whole specimen, upper view showing oscule. Scale: 1 cm; B. Whole specimen, side view showing the pore area. Scale: 1 cm; C. Thick section of ectosome and choanosome. Scale: 2 mm; D. Close-up of thick section showing the abundance of large plesiasters. Scale: 200 μ m.

The choanocyte chambers seemed a bit bigger (50–60 µm) for *T. schmidtii*, but not as much as the ones measured by Sollas (1888): up to 90 µm. Mediterranean specimens of *Thenaea* have raised doubts concerning the validity of *T. schmidtii*. Sollas (1888) described *T. intermedia* with few plesiasters associated with poorly developed choanosome tissue and large choanocyte chambers (with measurements intermediate between *T. schmidtii* and *T. muricata* from Norway). On the contrary, Topsent (1904) described a Mediterranean specimen with numerous plesiasters (as large as in *T. schmidtii*) associated with dense choanosomal tissue. Therefore, these characters have been considered to be variable and *T. schmidtii* was synonymized with *T. muricata* (Uriz 1981; Steenstrup & Tendal 1982). The Mediterranean specimen we examined is small (6 mm high, without the roots). It has numerous plesiasters, but not as large as in *T. schmidtii* (Table 5). Genetic data (Fig. 25) show that our Mediterranean specimen has the same COI and 28S sequence as *T. muricata* (ZMBN 85231) so Mediterranean specimens are likely to be *T. muricata* with numerous plesiasters. Meanwhile, even though *T. schmidtii* (ZMAPOR 18036) has the exact same COI Folmer fragment as *T. muricata*, its faster evolving 28S (C1–D2) sequence is significantly different (Fig. 25). This strongly suggests that *T. schmidtii* is a valid NEA species and that we are not focusing on the right characters to differentiate it. The amount of plesiasters and the size of the choanocyte chambers do not seem to be reliable characters; the size of plesiasters does not seem to be a good character as they can be fairly large in *T. muricata* as well (Table 5). The very large plesiasters (actins of 420–540 µm length) found by Babiç (1915) in *Thenaea* from the Adriatic Sea (Table 5) are puzzling at the moment. The white broad sphincter around the oscule of *T. schmidtii* might be a more reliable character, but we need more specimens to confirm this.

An even more southern species is *Thenaea bojeadori* von Lendenfeld, 1907 (and its possible synonyms *T. microclada* von Lendenfeld, 1907 and *T. megastrella* von Lendenfeld, 1907) which can be found all along the northern coast of Africa (Lévi 1959; Cruz 2002) (Fig. 22). The status of *T. bojeadori* would also need to be reevaluated in order to clearly separate it from *T. schmidtii* and *T. muricata* (Table 5).

TABLE 5. Depth, individual spicule dimensions of streptasters (in µm) for specimens of *Thenaea valdiviae*, *Thenaea muricata*, *Thenaea schmidtii* and *Thenaea bojeadori*. Means are in bold; other values are ranges; n=30 unless stated otherwise between parentheses. - = not referred.

Material	Depth (m)	Plesiaster (actin length)	Spiraster/metaster (length)
<i>T. valdiviae</i>	588–677	50–100	22–35
SE of Faeroe Islands, holotype (von Lendenfeld 1907)			
Boreo-arctic region (Steenstrup & Tendal 1982)	110–1900	30–100 (few)	20–40
ZMBN 85234 * Greenland Sea	578	25– 45 –70 (few)	20– 32.2 –42.5
ZMBN 85233 * Barents Sea	297	18.5– 41.4 –75 (few)	11– 18.2 –27.5
ZMBN 85257 * Røst reef, northern Norway	300	21.3– 49.9 –77.5	18.6– 24.9 –32 (10)
<i>T. muricata</i>	300	16.6– 37.0 –70.3	13– 23.2 –32.5
ZMBN 85231 * Korsfjord, western Norway			
Boreal region (Steenstrup & Tendal 1982)	90–2940	12.5–275	18–36
Gulf of Cadiz to western Mediterranean (Boury-Esnault <i>et al.</i> 1994)	110–2145	15– 69 –110	13– 22.6 –32
Off Cataluna, Spain (Uriz 1981)	100–480	25–100 (abundant)	15–30
Off Cataluna, Spain (Uriz & Rosell 1990)	1020–1322	20–80	19–23

..... continued on the next page

TABLE 5 (continued)

Material	Depth (m)	Plesiaster (actin length)	Spiraster/metaster (length)
MNHN-DCL3436 *	800	31– 126.9 –247	18– 25.2 –39
Banyuls France		(abundant)	(10)
Adriatic Sea (Babiç 1915)	-	420–540 (abundant)	21
Bay of Naples (Pulitzer-Finali 1972)	120	15–250	16–40
MNHN-DCL4083 *	585	24– 51.4 –92	14.8– 21.6 –37
young individual, southern Italy		(very abundant)	(10)
ZMBN 85254 *	544	19– 135.6 –280	15– 22.2 –30
Gulf of Cadiz		(abundant)	(10)
Balgim campaign			
<i>T. schmidtii</i>	713–1828	175–205	32
Gibraltar to Azores (Sollas 1888)		(very abundant)	
ZMAPOR 18036 *	443	20– 117.5 –210	14.8– 24.9 –37
Gulf of Cadiz		(very abundant)	(10)
<i>T. bojeadori</i>	146	30–110	15–17
Morocco (von Lendenfeld 1907)			
Ivory Coast (Lévi 1959)	–	17–250	15
Canary Islands (Cruz 2002)	Infra-littoral	20–320	20–24

* specimen measured for this study.

***Thenaea valdiviae* von Lendenfeld, 1907**

(Figures 18G–H, 24, Table 5)

Synonymy (modified from Steenstrup & Tendal (1982)).

Thenaea valdiviae von Lendenfeld, 1907: von Lendenfeld 1907, p. 190; Hentschel 1929, p. 863, p. 918; Steenstrup & Tendal 1982, p. 259; Klitgaard 1995, p. 1; Cárdenas *et al.* 2011, Table S1.

Thenaea muricata: Vosmaer 1882, p. 5; Vosmaer 1885, p. 4; Levinsen 1886, p. 343; Lundbeck 1909, p. 427; Brøndsted 1933, p. 6; Burton 1934, p. 6.

Thenaea muricata (in part): Stephens 1915, p. 11.

?*Thenaea muricata*: Hansen 1885, p. 18; Koltun 1966, p. 36.

Material. ZMBN 85255, west of Marstein, western Norway, 60°8'18"N, 4°50'47"E, 300 m, Agassiz trawl; ZMBN 85256, Freifjorden, Møre, western Norway, 63°02.09'N, 7°51.82'E, 100 m, Møre 2006 cruise; NTNU-VM 55620, Sandøy, Risværfjorden, 65°0'15.00"N, 11°29'30.00"E, 100–130 m; ZMBN 85257, near Røst reef, northern Norway, 67°35.23'N, 9°28.92'E, Polarstern ARK-XXII/1a 2007 cruise, 598 m; NTNU-VM 55545, Vågsfjorden, Vesterålen, northern Norway, 69°0'30.99"N, 16°40'52.99"E, 250–300 m; NTNU-VM, 54950, Barents Sea, 70°43'N, 16°56'E, 740 m; NTNU-VM 54975, Barents Sea, 70°46'N, 17°00'E, 910 m; ZMBN 85233, Barents Sea, off Finnmark, 'Ecosystem Barents Sea 2007' cruise, 71°48.32'N, 28°39.76'E, 297 m.

Comparative material.

Thenaea valdiviae, ZMAPOR 2385, Willem Barents Sea Expedition 1878–84, off Finnmark, northern Norway (71°52'0.11"N, 19°46'59.88"E), 324 m, identified by G. C. J. Vosmaer as *T. muricata*, det. P. Cárdenas; ZMBN 85234, Schultz Massive Seamount, Greenland Sea, 73°50'N, 7°32.3'E, BIODEEP 2007 cruise, 578 m, ROV.

Outer morphology (Fig. 24A–D). Massive sponge. Young specimens (ZMBN 85257) have cribriporal pores and a uniporal oscule on opposite sides (as in young *T. muricata*), with a flat top surface. A fringe surrounds the oscule. Budding was observed on the top surface of these young specimens (Fig. 24D). Larger specimens are sub-circular (ZMBN 85255, 85233) or slightly flattened (ZMBN 85256) with a triangular shape. They look very much like *T. muricata* but the oscule, separated from the poral area and situated on the top, always has a coarse sieve covering it. Surface is minutely to very hispid. Not compressible.

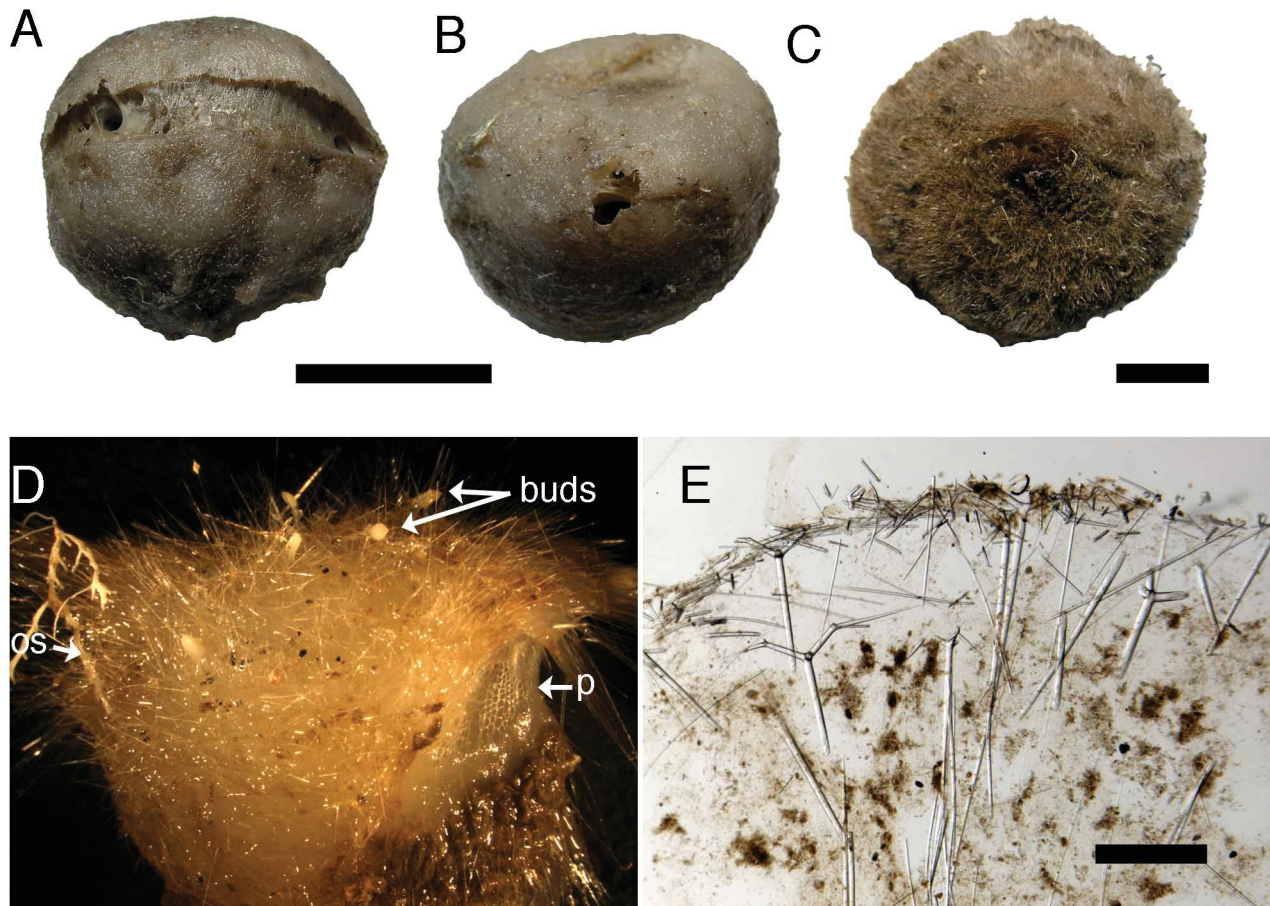


FIGURE 24. *Thenea valdiviae* von Lendenfeld, 1907. A. Whole specimen from Barents Sea, top view. Note the sieve on the oscule [ZMBN 85233]. Scale: 2 cm; B. Whole specimen, side view showing the poral area, also with sieve [ZMBN 85233]; C. Whole specimen from Freisfjorden (Møre), top view. Note the sieve on the oscule. Scale: 1 cm [ZMBN 85256]; D. Top surface of a young specimen covered with buds. p: pores. os: oscule. [ZMBN 85257]; E. Thick section showing the skeletal organization. Scale: 1 mm [ZMBN 85233].

Skeleton (Fig. 24E). Like *T. abyssorum*.

Spicules (ZMBN 85233) (Fig. 18G–H). (a) oxeas, slightly bent, length: 4–10 mm; width: 20–48.1–70 μm (N=8). (b) dichotriaenes, rhabdome is with a single bend, more rarely flexuous, most rhabdomes have a swelling just below the cladome, rhabdome length: 620–3933.7–5075 μm (N=8); width: 23–58.1–90 μm ; many irregular cladomes, protoclad length: 75–236.8–350 μm ; deutero-clad length: 125–600.2–1175 μm . (c) anatriaenes, rare, rhabdome straight or bent, length: 4000–4125 μm (N=2); rhabdome width: 15–20 μm ; bent clads (similar to *T. muricata* anatriaenes), clad length: 170–220 μm . (d) prototriaenes, not observed in this specimen. (e) spirasters (and rare metasters) (Fig. 18H), spined, length: 11–18.2–27.5 μm . (f) plesiasters (Fig. 18G), few, 4–6 actines, faintly spined, actine length: 18.5–41.4–75 μm , actine width: 3–7.4–12.5 μm (N=23).

Reproduction. Oocytes in vitellogenic phase were observed in the thick sections of ZMBN 85233, collected in mid–August 2007. Subglobular whitish buds were occasionally observed on specimens from the Røst reef (Fig. 24D) and from the Schultz Massive Seamount (Greenland Sea).

Distribution. Greenland, Iceland, Faeroe Islands, Norway, Norwegian Sea, Greenland Sea, Barents Sea, Spitzbergen (Steenstrup & Tendal 1982); SW of Ireland (Stephens 1915).

Depth. 100–1900 m (Steenstrup & Tendal 1982; this study).

Discussion. The specimens from the Korsfjord have more anatriaenes and regular dichotriaenes than ZMBN 85233 from the Barents Sea. Protriaenes are very common in ZMBN 85234 from the Greenland Sea. Plesiasters are rare (ZMBN 85233) to moderately present (ZMBN 85255, 85257).

T. valdiviae is known to be at least dimorphic and our Norwegian specimens correspond to the ‘arctic form’ described by Steenstrup & Tendal (1982). Our new records show that *T. valdiviae* must be present all along the Norwegian coast whereas, to our knowledge, *T. muricata* has not been formally identified north of Trollsteinen (64°35’N), except for the type.

The easiest way to discriminate adult specimens is to look at the oscule morphology: large cribriporal irregular shaped oscules with a surrounding fringe in *T. valdiviae*, small uniporal round “naked” oscules in *T. muricata*. Young specimens are, without genetic markers, very difficult to differentiate since they both have opposite oscule/pore areas on their sides. As for the spicules, they are fairly similar in both species (Table 5). There seems to be more metastars in *T. muricata* and *T. schmidtii* than in *T. valdiviae*, but this need to be confirmed. Moreover, the rarity of plesiasters in *T. valdiviae* seems to be a general rule, observed by others (Vosmaer 1885; Steenstrup & Tendal 1982).

As sister-species, Norwegian *T. valdiviae* are genetically clearly separated from *T. muricata* (Fig. 25), but our specimen from the Greenland Sea seamount is somewhat different (ZMBN 85234): it has a COI sequence identical to *T. muricata*, and on the other hand a 28S sequence identical to *T. valdiviae*. This specimen, and others examined from the same seamount are all very hispid (hairy-like), with cribriporal oscule and pores on opposite sides, and rare plesiasters. So they are not morphologically different from the Norwegian *T. valdiviae*, except maybe for the larger spirasters (Table 5). This shared COI could be the result of ongoing hybridization with *T. muricata* and deserves to be further studied.

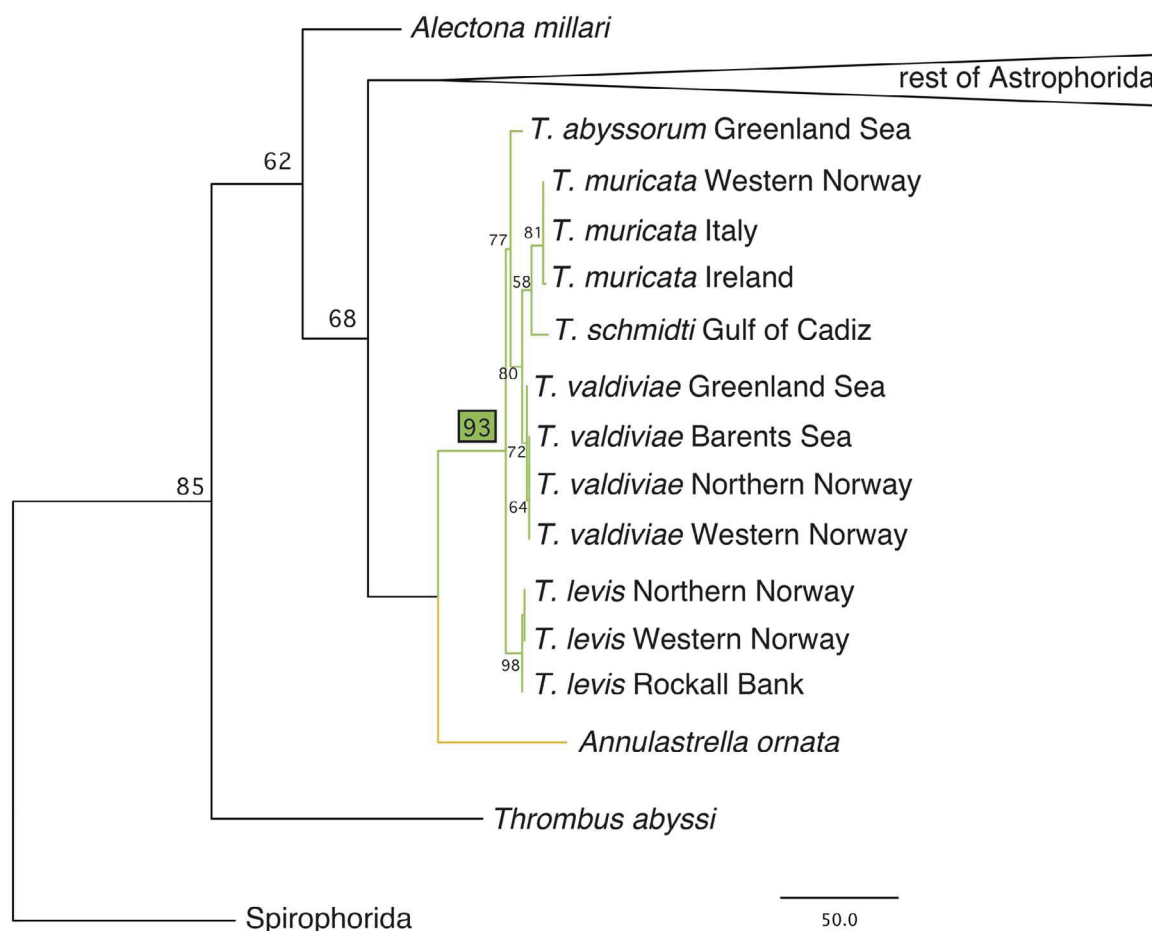


FIGURE 25. Simplified molecular phylogeny of the Astrophorida focusing on the relationships within the Theneidae, modified from Cárdenas *et al.* (2011, Fig. 2). Maximum-likelihood tree made from concatenated sequences of COI (Folmer fragment) and 28S (C1–D2 domains). Bootstrap nodal support values >50% are given above the nodes (2,000 replicates).

General conclusion and key

We here report and describe the eight Astrophorida species with streptaster microscleres which can be found in Norwegian waters, three of which are new for the area (*Vulcanella* cf. *aberrans* *Characella pachastrelloides* and *Pachastrella nodulosa* sp. nov.). *Thenia* species are present on soft sediments in deeper waters, extending throughout the boreo-arctic continental plateaus or seamounts (*T. muricata*, *T. valdiviae*, *T. levis*), abyssal plains (*T. abyssorum*), and in the deeper part of fjords (Figs. 20, 22). *Characella pachastrelloides*, *Poecillastra compressa* and *Pachastrella nodulosa* prefer current exposed hard-bottoms which can be found along the European/African continental slopes, seamounts and volcanic islands (e.g. Azores), or fjords (see for example the distribution of *C. pachastrelloides*, Fig. 3). In this type of habitat these sponge species are often found together with deep-sea corals (e.g. Røst reef, Mingulay reef, Rockall bank, Korsfjord). This habitat preference also explains their absence along the nearby Swedish and Danish coasts, as well as the North Sea, where hard substrate in deeper waters is very limited. The continuity between the European and African continental slopes probably accounts for the wide distribution of *Pachastrella monilifera* and *P. compressa* (Figs. 6, 13). This continuum of populations makes it difficult to reveal potential cryptic species, but the example of *Pachastrella nodulosa* shows that morphological divergences can be found, even in populations that colonized the Norwegian coasts quite recently (e.i. after the Last Glacial Maximum: 20,000 years ago). We suspect that similar divergences are present between *P. compressa* populations but more data is needed to reveal them.

As explained in the introduction, the Pachastrellidae *sensu* Maldonado (2002) is polyphyletic and genera with streptasters have now been reorganized in three families and three *incertae sedis* groups (Cárdenas *et al.* 2011). We present below a list of these genera with streptasters (in bold, genera that are present in the NEA/Mediterranean Sea):

Family Theneidae Carter, 1883

Annulastrella Maldonado, 2002

Cladothenia Koltun, 1964

Thenia Gray, 1867

Family Pachastrellidae Carter, 1875

Brachiaster Wilson, 1925

Nethea Sollas, 1888

Pachastrella Schmidt, 1868

Triptolemma de Laubenfels, 1955

Family Vulcanellidae Cárdenas *et al.*, 2011

Poecillastra Sollas, 1888

Vulcanella Sollas, 1886

Lamellomorpha Bergquist, 1968 *incertae sedis*

Characella Sollas, 1886 *incertae sedis*

Neamphius de Laubenfels, 1953 *incertae sedis*

Although streptaster microscleres are a plesiomorphy, they are still a useful starting point character to identify these Astrophorida species. The following key has been constructed to aid in the identification of the 26 streptaster-bearing Astrophorida species from the NEA/Mediterranean Sea.

Key for the species of streptaster-bearing Astrophorida from the North-East Atlantic/Mediterranean Sea (26 species, lithistids not included).

1.	Megascleres are triaenes (ortho- or dichotriaenes, long or short-shafted)	2
	Megascleres are mainly calthrops (a few pseudo-calthrops can be present).	3
	Megascleres are short-shafted mesotriaenes	4
	No megascleres, only annulate plesiasters	5
2.	Long-shafted triaenes (ortho- or dichotriaenes)	6
	Short-shafted triaenes (pseudocalthrops)	7
3.	Microxeas are annulate	8
	Microxeas (sometimes rare) are smooth	9
4.	Microscleres are coarsely spined microrhabds and amphiasters.	<i>Triptolemma intextum</i>
	Microscleres are minutely spined microrhabds and spirasters	<i>Triptolemma simplex</i>
5.	Abundant microxeas, plesiasters with actines up to 81 x 5.5 µm	<i>Annulastrrella verrucolosa</i>
	Rare microxeas, plesiasters with actines up to 200 x 16 µm.	<i>Annulastrrella ornata</i>
6.	Microxeas present	10
	Microxeas absent.	11
7.	Anatriaenes present.	<i>Poecillastra rudiastra</i>
	Anatriaenes absent.	17
8.	Choanosome is whitish; short-shafted triaenes.	<i>Vulcanella gracilis</i>
	Choanosome is gray, black or brown, short-shafted ortho/dichotriaenes	<i>Vulcanella</i> cf. <i>horrida</i> *
9.	Microstrongyles present	18
	Microstrongyles absent	<i>Nethea amygdaloides</i>
10.	Irregular triaenes and annulate microxeas (2–3 sizes)	<i>Vulcanella aberrans</i>
	Regular triaenes and annulate microxeas (1 size) <i>V.</i>	<i>ulcanella cribrifera</i>
	Regular triaenes and microxeas (1 size), not annulate	<i>Poecillastra symbiotica</i>
	Regular triaenes and microxeas (2 sizes), not annulate	16
11.	Elongated shape.	<i>Thenia levis</i>
	Sub-spherical, hemispherical or triangular shape	12
12.	Coarsely spined plesiasters and spirasters.	<i>Thenia abyssorum</i>
	Smooth or delicately spined plesiasters and spirasters	13
13.	Large cribriporal and irregularly shaped oscules	<i>Thenia valdiviae</i>
	Small uniporal and rounded oscules	14
14.	Plesiaster with actines up to 280 µm long.	15
	Very large plesiasters (actines up to 320 µm long)	<i>Thenia bojeadori</i>
15.	Broad sphincter around the oscule	<i>Thenia schmidtii</i>
	Narrow sphincter around the oscule	<i>Thenia muricata</i>
16.	Amphiasters with naked central shaft and 7–11 actines	<i>Characella pachastrelloides</i>
	Amphiasters often with actines on central shaft and 5–18 actines	<i>Characella tripodaria</i>
17.	Numerous streptasters (spirasters to metastasters)	<i>Poecillastra compressa</i>
	Few streptasters (mainly amphiasters) <i>Poecillastra saxicola</i>	
18.	Acanthorhabds present (18–25 µm)	<i>Pachastrella echinorhabda</i>
	Acanthorhabds absent ¹⁹	
19.	Most large calthrops are irregular (splitting of actines)	20
	Most large calthrops are regular (actines rarely split) ²¹	
20.	Dicho- and mesodichotriaenes present	<i>Pachastrella ovisternata</i>
	Only dichotriaenes present <i>Pachastrella chuni</i>	
21.	Large oxeas present.	<i>Pachastrella monilifera</i>
	Large oxeas absent	<i>Pachastrella nodulosa</i> sp. nov.

* The holotype of *V. horrida* from Florida has calthrops instead of short-shafted triaenes (Maldonado 2002), so the NEA species (Topsent, 1892;1904;1928) might represent a different species.

Acknowledgments

We dedicate this paper in the memory of Professor Christoffer Schander (1960-2012) who initiated this review by collecting the first specimen which started this study (*C. pachastrelloides*). We thank the crew of the R/V *Hans Brattström* for good assistance in collecting material in the Bergen area. We warmly thank Friederike Hoffmann (Max Planck Institute) for welcoming P. Cárdenas on the R/V *Polarstern* ARK-XXII/1a cruise in 2007. The shipboard party and crew of the R/V *Polarstern* is thanked, especially the *Jago* team, Jürgen Schauer and Karin

Hissman. We also thank Jeroen Ingels (Ghent University), Julie Reveillaud (Ghent University), Nina Mikkelsen (UoB) and Alexander Plotkin (UoB) for collecting additional material. Rob W. M. van Soest and Elly Beglinger hosted the visit of P. Cárdenas at the Zoological Museum (University of Amsterdam) thanks to the financial support of the European Commission's Research Infrastructure Action via the SYNTHESYS NL-TAF grant 5230. Thank you to Isabelle Domart-Coulon (MNHN), Marie Meister (Musée Zoologique de Strasbourg), Torkild Bakken and Anita Kaltenborn (NTNU-VM), Shirley Pomponi and John Reed (HBOI) for sharing specimens. Thank you to JNCC, Annika Clements, Jon Anders Kongsrud and Bergen University Museum for letting us use their underwater pictures of *P. compressa*. The molecular work was done with great support from the staff in the Biodiversity laboratories at UoB. Thank you to Egil Erichsen for technical assistance while using the SEM. Thank you to Aurelio Cárdenas for help in viewing and treating the video data from the JAGO manned-submersible. Manuel Madonado is thanked for valuable comments when reviewing this paper and for sharing samples and pictures of *V. aberrans*. This work was supported by grants to HTR from the 'Norwegian Deep Sea Program' and Statoil Hydro (contract no. 4501533230), The Norwegian Academy of Science and Letters, The Norwegian Biodiversity Information Centre (project no. 70184219) as well as the Norwegian Research Council through the Center for Geobiology. This is a publication of the Center for Geobiology, University of Bergen.

References

- Arnesen, E. (1932) Spongia. In: *Report on the Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910*. Bergen Museum, Bergen, pp. 1–29, pls I–V.
- Babić, K. (1914) Über *Ancorina* (*Thenaea*) *muricata* (Bowerbank). *Zoologischen Anzeiger*, XLV, 152–158.
- Babić, K. (1915) Zur Kenntnis der Theneen. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 40, 389–408, pl. 16–18.
- Babić, K. (1922) Monactinellida und Tetractinellida des Adriatischen Meeres. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 46, 217–302, pls 8–9.
- Barthel, D. & Tendal, O.S. (1993) The sponge association of the abyssal Norwegian-Greenland sea: species composition, substrate relationships and distribution. *Sarsia*, 78, 83–96.
- Bergquist, P.R. (1968) The Marine Fauna of New Zealand: Porifera, Demospongiae, Part 1. (Tetractinomorpha and Lithistida). *New Zealand Department of Scientific and Industrial Research Bulletin [New Zealand Oceanographic Institute Memoir 37]* 188, 1–105.
- Bo, M., Bertolino, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Pansini, M. & Taviani, M. (2012) Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. *Hydrobiologia*, 1–15. DOI: 10.1007/s10750-011-0964-1.
- Boury-Esnault, N. & van Beveren, M. (1982) Les Démosponges du plateau continental de Kerguelen-Heard. *Comité national français des recherches antarctiques*, 52, 1–175.
- Boury-Esnault, N., Marschal, C., Kornprobst, J.M. & Barnathan, G. (2002) A new species of *Axinyssa* Lendenfeld, 1897 (Porifera, Demospongiae, Halichondrida) from the Senegalese coast. *Zootaxa*, 117, 1–8.
- Boury-Esnault, N., Pansini, M. & Uriz, M.J. (1994) Spongiaires bathyaux de la mer d'Alboran et du golfe ibéro-marocain. *Mémoires du Muséum national d'Histoire naturelle*, 160, 1–174.
- Bowerbank, J.S. (1858) On the Anatomy and Physiology of the Spongiadae. Part I. On the Spicula. *Philosophical Transactions of the Royal Society of London*, 148, 279–332, pls XXII–XXVI.
- Bowerbank, J.S. (1866) *A Monograph of the British Spongiadae. Volume 2*. Ray Society, London, i–xx, 1–388 pp.
- Bowerbank, J.S. (1872) Contributions to a General History of the Spongiadae. Part I. *Proceedings of the Zoological Society of London*, 1872, 115–129, pls V–VI.
- Bowerbank, J.S. (1874) *A Monograph of the British Spongiadae. Volume 3*. Ray Society, London, i–xvii, 1–367, pls I–XCII pp.
- Bowerbank, J.S. & Norman, A.M. (1882) *A Monograph of the British Spongiadae. Volume 4 (Supplement)*. London, i–xvii, 1–250, pls I–XVII pp.
- Brattegard, T. & Holthe, T. (1997) Distribution of marine benthic macroorganisms in Norway. A tabulated catalogue. Preliminary edition, p. 409. In: Research Report from DN 1997-1. Directorate for Nature Management, Trondheim.
- Breen, O. (1990) *Oseanografi*. Gyldendal Norsk Forlag, 179 pp.
- Brøndsted, H.V. (1933) The Godthaab expedition 1928. Porifera. *Meddelelser om Grønland*, 79, 1–25.
- Burdon-Jones, C. & Tambs-Lyche, H. (1960) Observations on the fauna of the North Brattholmen stone-coral reef near Bergen. *Årbok for Universitetet i Bergen, Mat.-Naturv. Serie*, 4, 1–23.
- Burton, M. (1930) Norwegian sponges from the Norman collection. *Proceedings of the Zoological Society of London*, 1930, 487–546, pls I–II.
- Burton, M. (1931) Report on the sponges collected by Mr. Soot-Ryen in the Folden Fjord in the year 1923. *Tromsø Museums skrifter*, 1, 1–8.

- Burton, M. (1932) Sponges. In: *Discovery Reports, Vol. VI*. Cambridge University Press, Cambridge, pp. 237–392, pls XLVIII–LVI.
- Burton, M. (1934) Report on the sponges of the Norwegian expeditions to East-Greenland (1930, 1931, and 1932). *Skifter om Svaldbard og Ishavet*, 61, 1–33.
- Burton, M. (1954) Sponges. in: The 'Rosaura' Expedition. Part 5. *Bulletin of the British Museum (Natural History) Zoology*, 2, 215–239, pl. 9.
- Burton, M. (1959a) Sponges. In: *Scientific Reports. John Murray Expedition, 1933–34*. British Museum (Natural History): London, 151–281.
- Burton, M. (1959b) Spongia. In: Fridriksson, A. & Tuxen, S.L. (Eds.) *The Zoology of Iceland*. Ejnar Munksgaard, Copenhagen & Reykjavik, pp. 1–71.
- Cárdenas, P., Rapp, H.T., Schander, C. & Tendal, O.S. (2010) Molecular taxonomy and phylogeny of the Geodiidae (Porifera, Demospongiae, Astrophorida) — combining phylogenetic and Linnaean classification. *Zoologica Scripta*, 39, 89–106.
- Cárdenas, P., Xavier, J., Tendal, O.S., Schander, C. & Rapp, H.T. (2007) Redescription and resurrection of *Pachymatisma normani* (Demospongiae, Geodiidae), with remarks on the genus *Pachymatisma*. *Journal of the Marine Biological Association of the United Kingdom*, 87, 1511–1525.
- Cárdenas, P., Xavier, J.R., Reveillaud, J., Schander, C. & Rapp, H.T. (2011) Molecular phylogeny of the Astrophorida (Porifera, Demospongiae[®]) reveals an unexpected high level of spicule homoplasy. *PLoS ONE*, 6, e18318. doi:10.1371/journal.pone.0018318.
- Carter, H.J. (1876) Descriptions and Figures of Deep-Sea Sponges and their Spicules, from the Atlantic Ocean, dredged up on board H.M.S. 'Porcupine', chiefly in 1869 (concluded). *Annals and Magazine of Natural History*, 4, (105), 226–240; (106), 307–324; (107), 388–410; (108), 458–479, pls XII–XVI.
- Carter, H.J. (1883) Contributions to our Knowledge of the Spongiada. -Pachytragida. *Annals and Magazine of Natural History*, 5, 344–369, pls XIV–XV.
- Chombard, C., Boury-Esnault, N. & Tillier, S. (1998) Reassessment of homology of morphological characters in Tetractinellid sponges based on molecular data. *Systematic Biology*, 47, 351–366.
- Cruz, T. (2002) *Esponjas marinas de Canarias*. Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias, S/C Tenerife, 260 pp.
- Dendy, A. & Burton, M. (1926) Report on some deep-sea sponges from the Indian Museum collected by the R.I.M.S. 'Investigator'. Part I. Hexactinellida and Tetractinellida (pars). *Records of the Indian Museum*, 28, 225–248.
- Dickinson, M.G. (1945) Sponges of the Gulf of California. In: *Reports on the collections obtained by Alan Hancock Pacific Expeditions of Velero III off the coast of Mexico, Central America, South America, and Galapagos Islands in 1932, in 1933, in 1934, in 1935, in 1936, in 1937, in 1939, and 1940*. The University of Southern California Press, Los Angeles, pp. 1–55, pls. 1–97.
- Erpenbeck, D., Duran, S., Rützler, K., Paul, V., Hooper, J.N.A. & Wörheide, G. (2007) Towards a DNA taxonomy of Caribbean demosponges: a gene tree reconstructed from partial mitochondrial CO1 gene sequences supports previous rDNA phylogenies and provides a new perspective on the systematics of Demospongiae. *Journal of the Marine Biological Association of the United Kingdom*, 87, 1563–1570.
- Ferrer-Hernández, F. (1912) Notas sobre las esponjas de Santander. *Boletín de la Real Sociedad española de Historia Natural*, 12, 573–588.
- Ferrer-Hernández, F. (1914) Esponjas del Cantábrico. Parte 2. III. Myxospongia. IV. Tetraxonida. V. Triaxonida. *Trabajos del Museo Nacional de Ciencias Naturales, Ser. Zoológica*, 17, 1–46.
- Ferrer-Hernández, F. (1922) Más datos para el conocimiento de las esponjas de las costas españolas. *Boletín de pescas*, Sept. Oct. y Nov., 1–26, pl. 1–2.
- Fosså, J.H., Mortensen, P.B. & Furevik, D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*, 471, 1–12.
- Gamulin-Brida, H. (1969) A contribution to the study of the tetractinellid sponge *Thenea muricata* with special consideration of its importance in the bionomics of the Adriatic Sea. *Thalassia Jugoslavica*, 5, 89–93.
- Gray, J.E. (1867) Notes on the arrangement of sponges, with the descriptions of some new genera. *Proceedings of the Zoological Society of London*, 2, 492–558, pls XXVII–XXVIII.
- Hansen, G.A. (1885) Spongiadae. The Norwegian North-Atlantic Expedition 1876–1878. *Zoologi*, 13, 1–26, pls I–VII, 1 map.
- Hentschel, E. (1929) Die Kiesel- und Hornschwämme des Nördlichen Eismeers. In: Römer, F., Schaudinn, F., Brauer, A. & Arndt, W. (Eds.) *Fauna Arctica. Eine Zusammenstellung der arktischen Tierformen mit besonderer Berücksichtigung des Spitzbergen-Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahre 1898*. G. Fischer, Jena, pp. 857–1042, pls XII–XIV.
- Kent, W.S. (1870) On a New Anchoring Sponge, *Dorvillia agariciformis*. *Monthly Microscopical Journal*, 4, 293–295, pl. LXVI.
- Kirkpatrick, R. (1902) Descriptions of South African Sponges. Part I. *Marine investigations in South Africa*, 1, 219–232, pls I–III.
- Klitgaard, A.B. (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. *Sarsia*, 80, 1–22.
- Koltun, V.M. (1959) Donnaia fauna abissalnuich glubin Zhentrlnovo Poljarnovo basseina [Fauna from the abyssal of central

- polar basin]. *Doklady Akademii Nauk SSSR. Seriya: Biologiya*, 129, 662–665.
- Koltun, V.M. (1964) Sponges (Porifera) collected in the Greenland seas and from the region to the north of the Spitzbergen and Franz Josef Land, from expeditions of the 'F. Litke' 1955, 'Obb' 1956 and 'Lena' 1957 and 1958. Scientific results of the high- latitudes Oceanographic Expeditions to the northern part of the Greenland Sea and adjacent areas of the Arctic basin between 1955–1958. *Trudy Arkticheskogo i antarkicheskogo Nauchno-Issledovatel'skogo Instituta*, 259, 143–166.
- Koltun, V.M. (1966) Four-rayed sponges of Northern and Far Eastern seas of the USSR (order Tetraxonida). *Opredeliti Faunei SSSR 90. (Zoological Institute of the Academy of Sciences of the USSR: Moscow, Leningrad)*, 1–112, pls I–XXXVIII.
- Könnecker, G. (1973) Littoral and benthic investigations on the West coast of Ireland—I. (Section A: faunistics and ecological studies). The sponge fauna of Kilkieran Bay and adjacent areas. *Proceedings of the Royal Irish Academy*, 73, Section B, 451–472.
- Lambe, L.M. (1896) Sponges from the Atlantic coast of Canada. *Transactions of the Royal Society of Canada*, 2, 181–211, pls I–III.
- Lambe, L.M. (1900) Sponges from the coasts of Northeastern Canada and Greenland. *Transactions of the Royal Society of Canada*, VI, 19–48, pls I–VI.
- de Laubenfels, M.W. (1934) New sponges from the Puerto-Rican deep. *Smithsonian Miscellaneous Collections*, 91, 1–28.
- Lebwohl, F. (1914) Japanische Tetraxonida, I. Sigmaphora und II. Astrophora metastrosa. *Journal of the College of Sciences, Imperial University of Tokyo*, 35, 1–116, pls. I–IX.
- von Lendenfeld, R. (1894) Eine neue Pachastrella. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, 103, pl. I, 439–442.
- von Lendenfeld, R. (1897) Notes on Rockall Island and Bank-Reports. On the Spongida. *Transactions of the Royal Irish Academy*, 31, 82–88.
- von Lendenfeld, R. (1903) Porifera. Tetraxonida. In: Schulze, F.E. (Ed.) *Das Tierreich.*, Friedländer: Berlin, pp. vi–xv, 1–168.
- von Lendenfeld, R. (1907) Die Tetraxonida. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf der Dampfer Valdivia 1898–1899*, 11, i–iv, 59–374, pls IX–XLVI.
- Lévi, C. (1959) Résultats scientifiques des Campagnes de la 'Calypso'. Campagne de la 'Calypso' dans le Golfe de Guinée et aux îles Principe, São Tomé et Annobon. 5. Spongiaires. *Annales de l'Institut Océanographique*, 37, 115–141, pls 5–6.
- Lévi, C. (1964) Spongiaires des zones bathyale, abyssale et hadale. *Galathea Report. Scientific Reports of the Danish Deep-Sea Expedition Round the World, 1950–52*, 7, 63–112, pls. II–XI.
- Lévi, C. (1967) Spongiaires d'Afrique du Sud. (3) Tétractinellides. *Transactions of the Royal Society of South Africa*, 37, 227–256, pls XVII–XIX.
- Lévi, C. (1993) Porifera Demospongiae: Spongiaires bathyaux de Nouvelle-Calédonie, récoltés par le 'Jean Charcot'. Campagne BIOCAL, 1985. Résultats des campagnes MUSORSTOM. Volume 11. *Mémoires du Muséum national d'Histoire naturelle (A, Zoologie)*, 158, 9–87.
- Lévi, C. & Lévi, P. (1989) Spongiaires (MUSORSTOM 1 & 2). In: J. Forest (Ed.). Résultats des Campagnes MUSORSTOM, Volume 4. *Mémoires du Muséum national d'Histoire naturelle (A, Zoologie)*, 143, 1–260.
- Lévi, C. & Vacelet, J. (1958) Éponges récoltées dans l'Atlantique Oriental par le "Président Théodore Tissier" (1955–1956). *Revue des Travaux de l'Institut des Pêches maritimes*, 22, 225–246.
- Levinsen, G.M.R. (1886) Kara-Havets Svampe (Porifera). *Dijmphna-Togtets zoologisk-botaniske Udbytte*, 341–372, pls. XXIX–XXXI.
- Longo, C., Mastrototaro, F. & Corriero, G. (2005) Sponge fauna associated with a Mediterranean deep-sea coral bank. *Journal of the Marine Biological Association of the U.K.*, 85, 1341–1352.
- Lundbeck, W. (1909) The Porifera of East-Greenland. *Meddelelser om Grønland*, 29, 423–464, pl XIV.
- Maldonado, M. (1992) Demosponges of the red coral bottoms from the Alboran Sea. *Journal of Natural History*, 26, 1131–1161.
- Maldonado, M. (1993) The taxonomic significance of the short-shafted mesotriaene reviewed by parsimony analysis: validation of *Pachastrella ovisternata* Von Lendenfeld (Demospongiae: Astrophorida). *Bijdragen tot de Dierkunde*, 63, 129–148.
- Maldonado, M. (1996) On the presence of anatriaenes in Pachastrellidae (Porifera: Demospongiae): evidence for a new phylogenetic family concept. *Journal of Natural History*, 30, 389–405.
- Maldonado, M. (2002) Family Pachastrellidae Carter, 1875. In: Hooper, J.N.A. & van Soest, R.W.M. (Eds.) *Systema Porifera. A Guide to the classification of Sponges*. Kluwer Academic / Plenum Publishers, New York, pp. 141–162.
- Narayanaswamy, B.E., Renaud, P.E., Duineveld, G.C.A., Berge, J., Lavaleye, M.S.S., Reiss, H. & Brattegard, T. (2010) Biodiversity Trends along the Western European Margin. *PLoS ONE*, 5, e14295.
- Oug, E. & Rapp, H.T. (2010) Svamper - Porifera. In: *The 2010 Norwegian Red List for Species. Norwegian Biodiversity Information Centre*. Trondheim, Norway. pp. 183–190.
- Pansini, M. (1987a) Littoral Demosponges from the banks of the Strait of Sicily and the Alboran Sea. In: Vacelet, J. & Boury-Esnault, N. (Eds.) *Taxonomy of Porifera: from the N.E. Atlantic and Mediterranean Sea*. NATO ASI series, pp. 149–186.
- Pansini, M. (1987b) Report on a collection of Demospongiae from soft bottoms of the Eastern Adriatic Sea. *Publications of the Sherkin Island Marine Station*, 1, 41–43.
- Pansini, M. & Musso, B. (1991) Sponges from Trawl-Exploitable Bottoms of Ligurian and Tyrrhenian Seas: Distribution and Ecology. *Marine Ecology*, 12, 317–329.
- Pulitzer-Finali, G. (1972) Report on a collection of sponges from the Bay of Naples. 1. Sclerospongiae, Lithistida,

- Tetractinellida, Epipolasida. *Pubblicazioni della Stazione zoologica di Napoli*, 38, 328–354.
- Pulitzer-Finali, G. (1983) A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of Demospongiae hitherto recorded from the Mediterranean Sea. *Annali del Museo Civico di Storia Naturale Giacomo Doria*, 84, 445–621.
- Rapp, H.T. (2006) Calcareous sponges of the genera *Clathrina* and *Guancha* (Calcinea, Calcarea, Porifera) of Norway (north-east Atlantic) with the description of five new species. *Zoological Journal of the Linnean Society*, 147, 331–365.
- Rapp, H.T., Klautau, M. & Valentine, C. (2001) Two new species of *Clathrina* (Porifera, Calcarea) from the Norwegian coast. *Sarsia*, 86, 69–74.
- Reveillaud, J., Remerie, T., van Soest, R.W.M., Erpenbeck, D., Cárdenas, P., Derycke, S., Xavier, J., Rigaux, A. & Vanreusel, A. (2010) Species boundaries and phylogenetic relationships between Atlanto-Mediterranean shallow-water and deep-sea coral associated *Hexadella* species (Porifera, Ianthellidae). *Molecular Phylogenetics and Evolution*, 56, 104–114.
- Russ, K. & Rützler, K. (1959) Zur Kenntnis der Schwammfauna unterseeischer Höhlen. *Pubblicazioni della Stazione zoologica di Napoli*, 30, 756–787, pls XII–XIII.
- Sarà, M. (1958) Contributo all conoscenza dei Poriferi del Mar Ligure (1). *Annali di Museo Civico di Storia Naturale Genova*, 70, 207–244.
- Sarà, M. (1964) Poriferi di acque superficiali (0–3 m.) del litorale italiano. *Annali del Pontificio Istituto Scienze e Lettere S. Chiara*, XIV, 299–317.
- Schmidt, O. (1862) Die Spongien des adriatischen Meeres. (*Wilhelm Engelmann: Leipzig*), i–viii, 1–88, pls. 1–7.
- Schmidt, O. (1868) *Die Spongien der Küste von Algier. Mit Nachträgen zu den Spongien des Adriatischen Meeres (Drittes Supplement)*. Wilhelm Engelmann, Leipzig, i–iv, 1–44, pls I–V. pp.
- Schmidt, O. (1870) Grundzüge einer Spongien-Fauna des atlantischen Gebietes. (*Wilhelm Engelmann: Leipzig*), iii–iv, 1–88, pls I–VI.
- Sneli, J.-A. (1998) A simple benthic sledge for shallow and deep-sea sampling. *Sarsia*, 83, 69–72.
- van Soest, R.W.M. (1993) Affinities of the marine Demosponge fauna of the Cape Verde Islands and tropical West Africa. *Courier Forschungsinstitut Senckenberg*, 159, 205–219.
- van Soest, R.W.M., Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez, B., Hajdu, E., Pisera, A.B., Vacelet, J., Manconi, R., Schoenberg, C., Janussen, D., Tabachnick, K.R. & Klautau, M. (2010) World Porifera database, <http://www.marinespecies.org/porifera>. Available from <http://www.marinespecies.org/porifera> (accessed 20 January 2010)
- van Soest, R.W.M., Cleary, D.F.R., de Kluijver, M.J., Lavaleye, M.S.S., Maier, C. & van Duyl, F.C. (2007) Sponge diversity and community composition in Irish bathyal coral reefs. *Contributions to Zoology*, 76, 121–142.
- van Soest, R.W.M. & Stentoft, N. (1988) Barbados Deep-Water Sponges. In: Hummelinck, P.W. & Van der Steen, L.J. (Eds.) *Studies on the Fauna of Curaçao and other Caribbean Islands*. Uitgaven van de Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen, No. 122., Amsterdam, pp. 1–175.
- Sollas, W.J. (1882) The sponge-fauna of Norway; a Report on the Rev. A.M. Norman's Collection of Sponges from the Norwegian Coast. *Annals and Magazine of Natural History*, 5, 426–453, pl XVII.
- Sollas, W.J. (1885) A Classification of the Sponges. *Annals and Magazine of Natural History*, 5, 395.
- Sollas, W.J. (1886) Preliminary account of the Tetractinellid sponges Dredged by H.M.S. 'Challenger' 1872–76. Part I. The Choristida. *Scientific Proceedings of the Royal Dublin Society (new series)*, 5, 177–199.
- Sollas, W.J. (1888) Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876. *Zoology*, 25, 1–458, pls I–XLIV, 1 map.
- Steenstrup, E. & Tendal, O.S. (1982) The genus *Thenea* (Porifera, Demospongiae, Choristida) in the Norwegian Sea and adjacent waters; an annotated key. *Sarsia*, 67, 259–268.
- Stephens, J. (1915) Sponges of the Coasts of Ireland. I.- The Triaxonida and part of the Tetraxonida. *Fisheries, Ireland Scientific Investigations*, 1914, 1–43, pls I–V.
- Strömberg, T. (1970) Emergence of *Paramuricea placomus* (L.) and *Primnoa resedaeformis* (Gunn.) in the inner part of Trondheimsfjord (West coast of Norway). *Det Kongelige Norske Videnskabers Selskab*, 4, 1–6.
- Strömberg, T. (1971) Vertical and horizontal distribution of *Lophelia pertusa* (Linné) in Trondheimsfjorden on the West coast of Norway. *Det Kongelige Norske Videnskabers Selskab*, 6, 1–9.
- Tendal, O.S., Brattegard, T. & Rapp, H.T. (2001) Phylum Porifera, p. 36–51. In: Distribution of marine, benthic macro-organisms in Norway. A tabulated catalogue. – Research Report for DN 2001-3. Brattegard, T. & Holthe, T. (eds.). Directorate for Nature Management, Trondheim.
- Thomassen, J.H. (2009) Cladorhizid sponges from hydrothermal vents and cold seeps in the NE Atlantic Ocean. MSc. Thesis. University of Bergen, Bergen, 94 pp.
- Thomson, C.W. (1873) *The Depths of the Sea*. Macmillan and Co., London, 527 pp.
- Topsent, E. (1890a) Éponges de la Manche. *Mémoires de la Société zoologique de France*, III, 195–205.
- Topsent, E. (1890b) Notice préliminaire sur les spongiaires recueillis durant les campagnes de l'Hirondelle. *Bulletin de la Société Zoologique de France*, 15, 26–32, 65–71.
- Topsent, E. (1892) Contribution à l'étude des Spongiaires de l'Atlantique Nord (Golfe de Gascogne, Terre-Neuve, Açores). *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*, 2, 1–165, pls I–XI.
- Topsent, E. (1894) Étude monographique des spongiaires de France I. Tetractinellida. *Archives de Zoologie Expérimentale et Générale*, 3, 259–400, pls. XI–XVI.
- Topsent, E. (1904) Spongiaires des Açores. *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*,

25, 1–280, pls 1–18.

- Topsent, E. (1913a) Spongiaires de l'Expédition Antarctique Nationale Ecossaise. *Transactions of the Royal Society of Edinburgh*, 49, 579–643, pls I–VI.
- Topsent, E. (1913b) Spongiaires provenant des campagnes scientifiques de la 'Princesse Alice' dans les Mers du Nord (1898–1899 - 1906–1907). *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*, 45, 1–67, pls I–V.
- Topsent, E. (1928) Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert I^{er} de Monaco. *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*, 74, 1–376, pls I–XI.
- Topsent, E. (1938) Contribution nouvelle à la connaissance des Eponges des côtes d'Algérie. Les espèces nouvelles d'O. Schmidt, 1868. *Bulletin de l'Institut Océanographique, Monaco*, 758, 19–32.
- Tornes, M. (2008) Taksonomi og økologi hos kalksvamper (Porifera, Calcarea) assosiert med stortare (*Laminaria hyperborea*) på vestkysten av Norge. MSc. Thesis. University of Bergen, Bergen, 64 pp.
- Uriz, M.-J. & Rosell, D. (1990) Sponges from bathyal depths (1000–1750 m) in the Western Mediterranean Sea. *Journal of Natural History*, 24, 373–391.
- Uriz, M.J. (1981) Estudio sistemático de las esponjas Astrophorida (Demospongia) de los fondos de pesca de Arrastre, entre Tossa y Calella (Cataluña). *Boletín (Instituto Español de Oceanografía)*, 6, 8–58.
- Uriz, M.J. (1988) Deep-water sponges from the continental shelf and slope off Namibia (Southwest Africa): Classes Hexactinellida and Demospongia. *Monografías de Zoología Marina*, 3, 9–157.
- Vacelet, J. (1961) Spongiaires (Démosponges) de la région de Bonifacio (Corse). *Recueil des Travaux de la Station marine d'Endoume*, 22, 21–45.
- Vacelet, J. (1969) Éponges de la Roche du Large et de l'étage bathyal de Méditerranée (Récoltes de la soucoupe plongeante Cousteau et dragages). *Mémoires du Muséum national d'Histoire naturelle (A, Zoologie)*, 59, 145–219, pls I–IV.
- Vosmaer, G.C.J. (1882) Report on the sponges dredged up in the Arctic Sea by the 'Willem Barents' in the years 1878 and 1879. *Niederländisches Archiv für Zoologie Supplement*, 1, 1–58, pls I–IV.
- Vosmaer, G.C.J. (1885) The Sponges of the 'Willem Barents' Expedition 1880 and 1881. *Bijdragen tot de Dierkunde*, 12, 1–47, pls I–V.
- Vosmaer, G.C.J. (1894) Preliminary notes on some tetractinellids of the Bay of Naples. *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, 2, 269–286.
- Voultsiadou, E. (2005) Sponge diversity in the Aegean Sea: Check list and new information. *Italian Journal of Zoology*, 72, 53–64.
- Weslawski, J.M., Wlodarska-Kowalczyk, M. & Legezynska, J. (2003) Occurrence of soft bottom macrofauna along the depth gradient in High Arctic, 79° N. *Polish Polar Research*, 24, 73–88.
- Witte, U. (1996) Seasonal reproduction in deep-sea sponges-triggered by vertical particle flux? *Marine Biology*, 124, 571–581.
- Wörheide, G., Erpenbeck, D. & Menke, C. (2007) The Sponge Barcoding Project: aiding in the identification and description of poriferan taxa. In: Custódio, M.R., Lôbo-Hajdu, G., Hajdu, E. & Muricy, G. (Eds.) *Porifera research: biodiversity, innovation and sustainability*. Série Livros 28, Museu Nacional, Rio de Janeiro, pp. 123–128.
- Wright, P. (1870) Notes on Sponges. 1, On *Hyalonema mirabilis*, Gray. 2, *Aphrocallistes Bocagei* sp. nov. 3, On a new Genus and Species of Deep Sea Sponge. *Quarterly Journal of Microscopical Science*, 10, 1–9, pls. I–III.
- Xavier, J.R., Rachello-Dolmen, P.G., Parra-Velandia, F., Schönberg, C.H.L., Breeuwer, J.A.J. & van Soest, R.W.M. (2010) Cryptic diversity in a "cosmopolitan" excavating sponge: the *Cliona* aff. *celata* complex (Porifera, Clionidae). *Molecular Phylogenetics and Evolution*, 56, 13–20.